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DEVELOPMENT, ENERGETICS AND NUTRITION OF CAPTIVE PACIFIC BRANT (*BRANTA BERNICLA ORIENTALIS*, TOUGARINOV)

A

DISSERTATION

Presented to the Faculty of the

University of Alaska in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

by

Keith A. Morehouse, B.S., M.S.

Fairbanks, Alaska

May 1974

DEVELOPMENT, ENERGETICS AND NUTRITION OF CAPTIVE PACIFIC BRANT

(BRANTA BERNICLA ORIENTALIS, TOUGARINOV)

RECOMMENDED:

Chairman, Advisory Committee

APPROVED:

Director, Institute of Arctic Biology

14 May 1974
Date

Vice President for Research

17 May 1974
Date

ABSTRACT

The development of young Pacific Brant (B. b. orientalis), energy relationships of young and adults and nutrition of brant utilizing eelgrass was studied in Fairbanks, Alaska on birds obtained from the breeding grounds of the Yukon-Kuskokwim Delta. Gosling growth rates were rapid with weight gain temporarily slowed by remige development. Feather growth curves were regular with secondaries and rectrices following the primary growth pattern closely; growth rate of primary 8 exceeded that of primary 9 during development. Subadult maximum and minimum yearly weights occurred in November and April, respectively. Thermoneutral winter oxygen rates were similar for both sexes; rates of males exceeded those of females. Winter metabolic rates of both sexes exceeded summer rates and were above predicted rates; summer rates were comparable to those predicted. Below the lower critical temperature, metabolism increased linearly with decreasing ambient temperature in both seasons; slopes were not different. Metabolism below the critical temperature was significantly higher in winter than in summer. Body temperature averaged 40.9°C and was not labile from -50 to +30°C. Heart rate increased linearly with decreasing ambient temperature below the critical temperature. Summer existence energy expenditure per bird and per gram body weight of females was greater than that of males. Gross activity pattern was highly random during the summer. Digestive efficiency did not change significantly with ambient temperature. Diets containing three levels of eelgrass fed to goslings were ineffective in producing

consistent or significant weight increases which was attributed to unacceptability. Only control ration and 50% eelgrass produced positive feed efficiencies; positive efficiencies of utilization were obtained with control, 50% and 75% eelgrass diets. Digestive efficiency decreased significantly as the eelgrass in the diets increased. Eelgrass nutrient constituent levels changed little over the collection period of 15 April to 19 November while caloric values decreased. Protein levels were consistently under dietary recommendations for geese.

ACKNOWLEDGEMENTS

I appreciate the continued and critical guidance of George C. West throughout the study. Stephen R. Johnson served as an interim advisor during Dr. West's sabbatical. I would also like to express my gratitude to others who provided assistance during the course of this study. Some of the agencies and individuals meriting special recognition are the U. S. Fish and Wildlife Service, particularly the staffs of the Clarence Rhode and Izembek Lagoon National Wildlife Ranges, for providing critical logistical support; Anne McClanahan and Beth Smith for care of goslings, Dave Kryzer for making feather measurements; the animal quarters' personnel at the Institute of Arctic Biology for veterinary and animal husbandry aid; Dan Holleman for statistical counselling and computer instruction; A. M. Gau and Diane Shaw for analytical services; Candy Anderson and Don Borchert for typing and graphical services, respectively; and fellow graduate students, Steven J. Person and William Arvey, who offered their warm friendship and also provided much thought provoking conversation. I gratefully acknowledge the understanding that has been given by my family during the course of this study.

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INTRODUCTION

Evans and Miller (1968) have recently stated, "the number of species whose nutritional requirements are known with any precision is relatively few. Of the mammals, only about a dozen species have been studied out of a total of over 5,000; the situation with birds is worse." On the other hand, there is an impressive accumulation of caloric relationships developed for both feral and domesticated birds. Students of avian biology have available to them a plethora of information on the nutrient requirements of some commercially important galliforms, somewhat less is available for certain anseriforms, and little for members of other groups.

Similarly little study has been devoted to investigation of the caloric and nutrient requirements of those forms which exhibit a high degree of dietary specialization. It should be expected that, just as the long-established diet of a species has a selective influence on the structure and function of a bird's feeding equipment (Welty, 1962), specialization will result in some modification of nutritional requirements. Consequently, conditions which bring about alterations in habitat or a source of nutrition may seriously jeopardize biological success.

Among waterfowl, few have exhibited a greater apparent dependence on a single food resource than the brant geese (Branta bernicla). Past declines in population numbers have been attributed to the reduction of available stocks of eelgrass (Zostera marina L.) generally throughout the bird's range, evidence which seems to support the concept that the

brants' specialization has resulted in some nutritional dependency on eelgrass.

Brant geese are described as being maritime in habit and circumpolar in their distribution, breeding farther north than any other geese but nevertheless wintering in temperate or subtropical regions. Although the taxonomy of brant geese continues to be controversial, the available evidence indicates a proper division of this group into 4 subspecies (one of which appears to be extinct) and the recommendation of recognizing the Pacific form as Branta bernicla orientalis, Tougarinov (Delacour and Zimmer, 1952) has been followed.

In the pre-nesting migration Pacific Brant disperse widely, to points as far west as the mouth of Khatanga River (110° E Long.) in Siberia and as far east as 110° W Long. in the Canadian Archipelago (Delacour, 1954). The Yukon-Kuskokwim Delta of Alaska is thought to contain the highest concentration of breeding brant at the present time (Einarson, 1965). As far as is presently known, post-nesting migration brings almost the entire population funneling through the eastern Bering Sea to Izembek Lagoon, Alaska, where the brant pause for a 2 month period before continuing southward.

Although the wintering areas of Pacific Brant include the coast of California, with scattered groups north to Oregon, Washington and British Columbia, the greatest concentrations are now found along the west coast of Baja California (Chamberlain et al., 1971). Previously, wintering areas of Pacific Brant have included the coasts of China and Japan but recent reports of sightings in these waters have become rare

(Leopold and Smith, 1953). In mid-winter there is a gradual movement of more southern populations northward to the general vicinity of Puget Sound, terminating in a buildup of brant numbers which anticipates a more massive return of breeding birds to subarctic and arctic nesting grounds via Izembek Lagoon (Einarson, 1965).

Except for the 2.5 to 3 month period of breeding ground residency during which the diet of adults changes to sedges and grasses (Barry, 1967; C. Lensink, pers. comm.), the brant have been observed to subsist almost wholly on eelgrass. Eelgrass (Zostera marina), one of many seagrasses, is not a true grass but a marine monocotyledonous angiosperm of the family Potamogetonaceae. Various parts of the plant are used by waterfowl but only Pacific Brant appear to take leaves selectively (Jones, unpubl.). Izembek Lagoon on the Alaskan Peninsula contains the most extensive stand of eelgrass reported (McRoy, 1970) and is certainly an important fall and spring feeding area for Pacific Brant. Beds used throughout the winter period are also significant in their contribution to brant subsistence.

It has been long reported that brant geese are closely "tied" to eelgrass dietarily but there is a lack of information on what the extent of the relationship is and how it relates to their nutrition and energy demands within their annual program. This study was undertaken to answer questions concerning brant energetics and nutrition.

In addition, awareness of an ever increasing marine pollution, which accompanies coastal development, injects a sense of urgency into the realization of a more complete definition of the brant-eelgrass relationship.

As with other waterfowl, there is a substantial literature on the feeding habits of brant geese. Among the numerous workers providing observations that identify eelgrass as a dietary item for brant are Bent (1925), Butcher (1934), Martin and Uhler (1939), Moffitt and Cottam (1941), Cottam et al. (1944), Gabrielson and Lincoln (1959) and Einarson (1965). Some investigators have provided more quantitative data on dietary components and their relative importance through collection of ingesta (Moffitt, 1941; Cottam et al., 1944) and analysis of excreta (Ranwell and Downing, 1959); the results of these investigations, and other recent information reviewed by Jones (unpubl.), indicates that the diet of the brant is more varied than has been supposed. Sincock (1962) and Burton (1961, 1962) have constructed formulae which estimate daily dry matter intake on the basis of percent of whole body weight (wet) for brant geese, this procedure was proposed to measure the impact of wintering birds on their food resources.

Energy requirement investigations with birds of a wide spectrum of size are proceeding at a rapid pace and are motivated mainly by the desire to identify and define bird-environment energy relationships. Of the waterfowl, investigations of energy requirement have been conducted with adult wild geese (Williams, 1965) to determine distributional and migrational constraints, and with teal (Owen, 1970) to define cage and field energy cost differences through a physiological indicator (heart rate). The heart rate and metabolism relationship was also investigated in this study to determine its reliability for possible use in the field and laboratory to indicate metabolic performance.

Cain (1973) has recently determined the energy costs of cage existence in tree ducks, at various temperatures, in order to assess the latitudinal restrictions for this species. Aside from the work on young brant in this study, which investigated relative efficiencies of pelleted commerical, eelgrass and part eelgrass diets, the only recent nutritional work with growing and developing wild species of waterfowl has been undertaken by Penney and Bailey (1970). Other work concerning waterfowl energetics has been reported by Benedict and Lee (1937) on the domestic goose (Anser anser) and, more recently, Lefebvre and Raveling (1967) have related the distribution of large and small Canada Geese (Branta canadensis) to differences in heat loss. In this study, energy balance trials yielded information on minimum energy requirements over an abbreviated range of temperatures above the lower critical temperature of summer brant, the results approximate what would be found for birds on the breeding grounds in western Alaska. An opportunity was also provided to compare energy balance data with that obtained via oxygen consumption experiments.

Smith and Prince (1973) investigated fasting metabolic rates of Mallards (Anas platyrhynchos) acclimatized to low ambient temperatures in order to determine their ability for northern wintering. The Pacific Brant's metabolic adaptations for northern life were investigated in both summer and winter respiratory metabolism trials by Irving et al. (1955); basic metabolic capabilities of Pacific Brant were investigated through oxygen consumption trials in this study as well. Hartung (1967) has recently reported oxygen consumption rates of Mallards and Black

Ducks (Anas rubripes having contaminated and uncontaminated plumages to determine the possible metabolic consequences of oil pollution. Other wild waterfowl for which metabolic rates have been published are the Trumpeter Swan (Cygnus cygnus buccinator) (Benedict and Fox, 1927) and the Wood Duck (Aix sponsa) (Herzog, 1930).

Nutritional studies with domesticated waterfowl have been carried out mainly on behalf of industry, these investigations have provided most of what is known about organic and inorganic nutrient metabolism and requirements. Holm and Scott (1954) have reported that the protein requirement of wild surface feeding and diving ducks was approximately 20 percent of the dry matter of the feed.

Major physiological studies of waterfowl are relatively few in number, the major contribution on domestic stock reported is that of Benedict and Lee (1937) and that for wild birds has been reported by Hanson (1958, 1962).

Eelgrass has been put to a variety of human uses, few of which have been dietary. However, it has become known quite recently that the seeds of Zostera were once an important and traditional source of food for the Seri Indians of the Gulf of California (Felger and Moser, 1973). Eelgrass fragments have been found in ancient fire sites, which suggested that eelgrass constituted a source of salt and soda. Near the turn of the present century feeding experiments were undertaken to determine the nutritive value of eelgrass for dogs and poultry (Burkholder and Doheny, 1968). Bauersfeld et al. (1969) have carried out feeding trials with livestock which resulted in increased gains when fed seagrass

supplemented diets.

The extent to which eelgrass is important in the energetics and nutrition of Pacific Brant should be reflected in its chemical composition, as well as the caloric yield. Organic constituent analyses have been made by Candussio (1960), Burkholder and Doheny (1968), and Udell et al. (1969). Einarson (1965) provided a comparison of crude protein values from Alaska, Washington, Oregon and California, while McRoy (1970) reported protein values from a number of Alaskan sites. Both McRoy (1970) and Udell et al. (1969) have reported caloric data for collected Zostera samples. This study provides chemical constituent and caloric values for a time series of collections from a single Alaskan location.

Lastly, an understanding of the normal growth and development of the experimental animal is basic to any meaningful nutritional or energetic study and consequently that information was sought for Pacific Brant as well.

In summary, the objectives of this study were to investigate growth and development of young Pacific Brant, energy relations of young and adults and the nutrition of brant utilizing eelgrass.

MATERIALS AND METHODS

Growth and Development

Brant used throughout these studies were field collected from wild populations and hand raised by the author. Early stage pipped eggs were obtained on 30 June 1971 and 30 June 1972 from nests of Pacific brant located on tidal flats adjacent to the mouth of the Kashunuk River on the Yukon-Kuskokwim Delta, Alaska (65°18'N, 165° 38'W). Eggs were hand carried to Fairbanks, Alaska (64°52'N, 147°50' W) in a wooden crate within 24 hours of collection; hatching occurred enroute. Therefore all birds, in each year, were the same age on any date and at the same approximate point of development.

Goslings were placed in a brooder cabinet and provided with a heat lamp that maintained air temperature at 30°C. The young birds were attended 24 hours/day for the first 5 days after hatching. The young brant were fed moistened Startina (Ralston-Purina Co.), crumbled hard-boiled eggs, and chopped grain seedlings during the first week. After the first week the egg supplement was omitted. Startina (Protein$\geq$ 30%) was replaced by Purina Game Bird Flight Conditioner (Protein$\geq$19%) as the main dietary item in the third week of feeding. When not on experimental diets, the latter commercial ration was fed exclusively. Startina was not employed for feeding young brant in the second summer of the study.

When 9 days old, the group of 20 goslings used for weight, tarsus and culmen measurements was placed in an inside-outside, concrete floored

pen and provided with food, water and a heat lamp; after day 57 the number of birds in this group was reduced to 13. Culmen and tarsus measurements were continued until day 57 while weight records were maintained for one year. Initially, 10 birds were selected for measurements from the 20 available. Weighings were made at 2 to 5 day intervals; after day 57, weighings were made less regularly on the 13 remaining birds but occurred at least once per month. As a pronounced diurnal weight cycle has been reported in some birds, weights were taken at approximately the same time each day (Baldwin and Kendeigh, 1938). For the first 21 days, birds were weighed to the nearest 0.1 g on a Torbal torsion balance, thereafter weights were recorded to the nearest 5 g using a hanging Chatillon autopsy scale.

Length of tarsus and exposed culmen were measured with a vernier caliper (Baldwin, Oberholser and Worley, 1931). Tarsal measurement was made with the leg in a flexed position. Tarsal length, as here defined, extends from the most anterior point of the tarso-metatarsal-phalangeal crest to the most posterior edge of the tarso-metatarsus at its lateral surface; the limits of the latter are clearly apparent behind the swelling of the tuberosity. Culmen length, or "chord of exposed culmen", was measured from the anterior surface of the nail, along the midline, to the mandible-forehead intersection at the point of the vee (Baldwin, Oberholser and Worley, 1931).

Eight goslings utilized for rectrix and remex measurements were among a larger group placed in outdoor, wire-floored cages on day 16; they remained in these units for the duration of this study. Measurement

of flight feather growth began when the feathers appeared, at day 10, and consisted of length measurements of the right primaries, secondaries, and rectrices weekly for 6 weeks. Measurements were made on flattened feathers with a flexible, transparent millimeter ruler from the skin where the calamus protrudes to the base of the natal down feather until it was lost and to the most distal point of the vane thereafter. Remiges were numbered from the wrist outward for primaries and inward for secondaries; rectrices were numbered starting with the outermost and proceeding inward.

Oxygen Consumption Experiments

Brant used in the 2 series of oxygen consumption tests were obtained in the summer of 1971. The brant were about 9 months old (subadults) when winter tested and about 2 years old (adults) when summer tested. Test birds were maintained in inside-outside cages in the large animal section of the Institute of Arctic Biology animal quarters' throughout the year. Outside temperatures ranged from -45.0 to +5.0°C and averaged -13.2°C over the period of winter testing (Jan., Feb.). Because birds remained in the inside section of the cage, temperatures to which they were exposed were considerably warmer and averaged +9.5°C. During the summer tests, outside temperatures to which the birds were acclimatized ranged from +2.0 to 29.0°C and averaged +15.0°C.

A commercial formulation (Game Bird Flight Conditioner) was fed exclusively as the basic diet, with greens and vitamins provided as supplements. Metabolic determinations were made on birds which were 8-12 hours postabsorptive. Both winter and summer tests were conducted

between 1700 and 2400 hours. Oxygen consumption was measured over an ambient temperature range of -80 to +40°C in an open circuit system using a Beckman F-3 paramagnetic oxygen analyzer (Morrison and West, 1974). In these experiments, a large capacity pump with regulatory valve and dry flow meter was employed to ventilate the metabolic chamber system. A smaller pump withdrew air from the higher flow capacity system and passed it in sequence through a dessicant only in the winter series and dessicant as well as a carbon dioxide absorber in the summer series, through a low-flow bypass to the oxygen analyzer and, finally, out via a wet-test flow meter. Flow rates were sums of those clocked at each flow meter and varied between 10 and 15 liters/min.

Standard gas mixtures including room air, analyzed by a Beckman E-2 oxygen analyzer, were used for recorder reference percentages. Calculations of oxygen consumption at STP were made using the appropriate formulae given by Depocas and Hart (1957).

At the beginning of each test, birds were weighed to the nearest 5 g and placed in a metal chamber, which in the winter series was a cylindrical steel can (42 cm high x 36 cm diameter) and in the summer series an aluminum box (34 cm wide x 49 cm long x 46 cm deep). Birds rested on a wooden board on the bottom of the chamber. Birds were also weighed at the termination of the experiment and the body weights were averaged for purposes of calculating metabolic rates on a body weight basis.

The metabolic chamber, with its air inlet on top and outlet at the bottom, was placed in a Missimer constant temperature unit where

temperatures in the metabolic chamber were controlled to ±1.5°C

Thirty-six guage copper-constantan thermocouples were variously placed to obtain temperatures inside and outside the metabolic chamber and within the cloaca of the bird; temperatures were recorded on a Leeds and Northrup 20-point recorder.

The duration of each metabolic run varied from 1 to 3 hours, dependent upon the length of time required for chamber temperatures to stabilize and the bird to reach an acceptably passive state as reflected in oxygen consumption recording variations. Each bird was tested at a single temperature and not used again for a period of 4 or 5 days.

During oxygen consumption trials heart rate frequency was recorded with a Hewlett-Packard 1500A Electrocardiograph prior to the termination of the trials when brant had reached stable, and usually, minimum levels of metabolism. Attachment of terminals to the birds was through use of gold-plated safety pins, two of which were attached bilaterally through the patagia and the third through the skin of the back. One or more of the leads were often broken by the birds' movements, especially at lower temperatures.

Summer Feed Studies and Adult Energy Balance

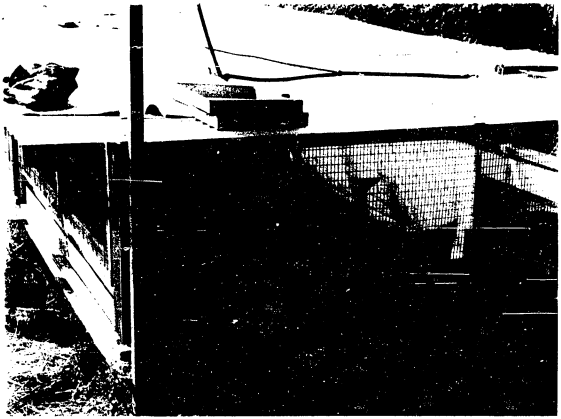
The gosling brant eelgrass feeding experiments and adult energy balance trials were conducted during the summers of 1972 and 1973 respectively. Summer feeding experiments were carried out with young brant maintained in groups of 5 in sheltered cages located in a fenced area 400 m north of the nearest permanent facility of the University

of Alaska campus in a clearing in a black spruce (Picea mariana) forest. Birds could not see campus lights and were disturbed only twice a day for feeding. The 4 cage units (each 2.4 x 1.8 x 0.6 m) used in the study had double swing-down doors which allowed easy access to the interior of each cage (Fig. 1). Excrement and spilled feed were collected on heavy duty polyethylene sheets placed beneath the welded wire floor. Wainscoting with a beveled and sheet-metal covered inner surface prevented loss of feces around the periphery of the floor. Cage dividers in the units were of solid plywood, sides were largely welded wire, the roof was constructed of transluscent ripple fiberglass which provided lighting of natural photoperiod but reduced intensity and the entire unit was supported 0.4 m off the ground on modified steel fence posts.

Birds were presented with experimental diets at 13 days of age and the study continued for 43 days. Diets involved in feeding trials were pelleted 100 percent commercial feed, 100 percent eelgrass, 50 percent eelgrass and 50 percent commercial feed, and 75 percent eelgrass and 25 percent commercial feed. Combination diets were made up on a dry weight basis of ground materials, which were subsequently pelleted with a California pellet mill using a 3/16 inch die. Early studies by Heuser and Scott (1951) indicate that there is a significant feed efficiency advantage (units of feed consumed per unit of weight gained) in pellet feeding over mash feeding of waterfowl. Feed and water were available ad libitum.

Representative samples of pelleted feeds were oven dried to determine

Figure 1. Gosling feed study double cage units.



water content and the appropriate correction was made for calculation of dry weight of food consumed. Caloric determinations were carried out on duplicate or triplicate samples ground in a Wiley Mill to pass through a 60 mesh/inch screen.

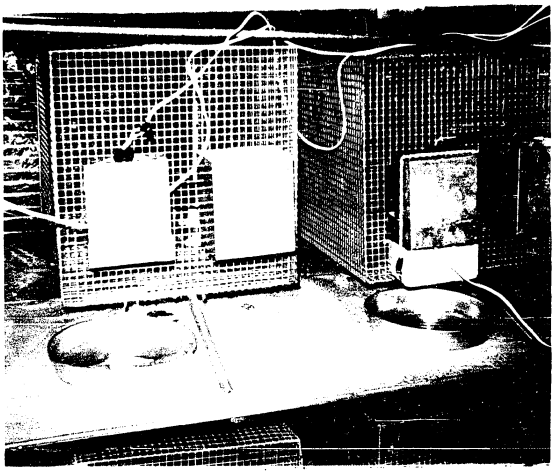
Each group of birds was maintained on a diet from 3 to 6 days in each trial. An attempt was made to maintain the size of a test group at 5 birds. Difficulty associated with maintaining birds on certain of the experimental diets, coupled with insufficient numbers of available birds due to mortality and debilitating injuries, precluded testing all groups at full complement and on all 4 diets simultaneously. During the course of the feeding trial period the goslings were developing a feather cover and not undergoing any significant degree of molt.

Individual body weights were taken before and after each trial period. Uneaten pelleted rations and excrement were collected at the end of the trial periods and air dried at room temperature. Excrement collections were often mixed with down and contour feathers which were removed prior to weighing and caloric determinations.

Metabolized energy (ME) was calculated by subtracting the total caloric value of excreta (Excretory Energy, EE) produced from the total value of feed ingested (Gross Energy Intake, GEI) (Kendeigh, 1949).

Energy balance trials were conducted with adult brant during the period 8 May to 24 June 1973 in the same caging area as previously described. During the course of the experiments, the birds were individually confined in welded cages measuring 0.4 x 0.4 x 0.8 m (Fig. 2). Birds were able to move about freely and assume normal preening

Figure 2. Adult energy balance study individual cage units.



positions. Each cage was suspended from a single, centrally located screw (in a teflon ball-socket arrangement) which allowed the cage to tilt both from end to end and side to side. Cage suspension was from a 1-1/4 inch steel pipe. Across both cage ends but at a lower level than the main support pipe, 5/8 inch conduit was placed to prevent gross cage movement (Fig. 2).

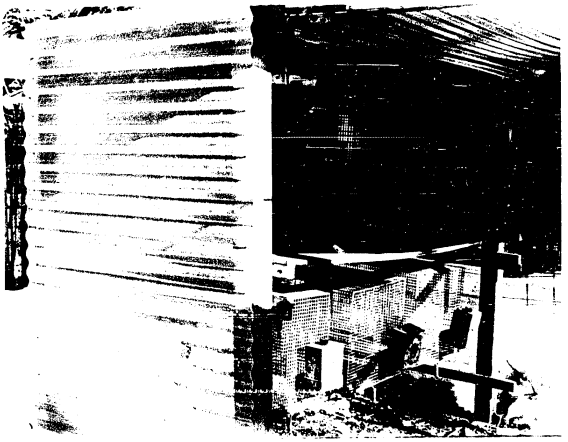
A microswitch attached to the conduit cage support was activated by cage movements which gave a continuing activity record throughout the trial period for each of 3 cages on an Esterline-Angus event recorder. The number of five minute intervals/hour/bird in which some activity (on a scale of 0 to 12) occurred was used to construct an index of activity. The unit in which the energy balance cages were mounted is shown in Fig. 3; inside dimensions are 2.1 x 1.5 x 2.0 m.

Trials were made over five day periods alternating with two day periods which allowed for cleaning cages and readying the facility for the following trial. Birds were weighed (to the nearest 5 g) at the beginning and termination of a trial at the same time of day. Excrement and uneaten food was dried at room temperature for a five day period and then weighed to the nearest 0.1 g. Geese in this study and other waterfowl (R. B. Owen, Jr., pers. comm.), carry food to the water dish which can result in a substantial source of error. Therefore, food in the water dish was transfered to the spill pan, oven dried overnight and weighed.

Molt was recorded after each trial by subjectively characterizing it as very heavy, heavy, moderate or light for individual birds.

Maximum and minimum daily temperatures were recorded inside the

Figure 3. Fiberglass covered main unit housing individual cages used in adult energy balance study.



cage housing.

Eelgrass Collection

Eelgrass (Zostera marina) was collected in order to determine changes in caloric and nutrient content and for use in feeding experiments. Samples were taken from eelgrass beds in Izembek Lagoon, located at the SW terminus of the Alaska Peninsula (55°N, 163°W) in early June 1972. Collection sites were marked with steel stakes in beds located approximately 400 m apart in areas that could be easily sampled on foot from the shore.

Eleven collections (22 samples) at approximately 2 week intervals were made during the period 30 May to 15 November 1972. On 15 April and 16 May 1973 two collections (4 samples) were made to supplement the series taken in the previous year. Samples were taken from green, rooted plants in beds just exposed at the lowest point of low tide. In this way, material could be chosen from the most densely vegetated areas at the site. An attempt was made to select fronds with attached organisms, as they appear to be preferred by brant observed in Izembek Lagoon (R. D. Jones, Jr., unpubl.), however, rhizomes accompanying the fronds in the collection operation were retained after first washing lightly to dislodge and remove sediments.

Collections of about 1 to 2 kg wet weight made at each site were placed in individual polyethylene bags and labeled. Samples were frozen, packed in a styrofoam insulated carton and air freighted to the laboratory in Fairbanks where they were thawed and air dried at 35.5 to 37°C within one week. Relative humidity at the drying site, as measured with a Sensuii wet-dry bulb hygrometer, fluctuated between 10 and 15 percent

and only rarely reached 20 percent in response to extremely high outside humidity. Drying time for these samples, spread loosely on polyethylene sheets, was approximately 6 to 8 hours to reach a moisture content level of 8 percent or less. Dried samples were reduced in volume by grinding in a Christie and Norris burr mill, followed by brief homogenization in a Waring blender and final grinding in a Wiley Mill fitted with a 60 mesh/inch screen.

Calorimetric determinations on duplicate samples were carried out with a Parr automatic adiabatic oxygen-bomb calorimeter. Protein was calculated from nitrogen determinations (N·6.25) made on a Model 185 Hewlett Packard CNH analyzer and total lipids were obtained by means of Soxhlet extraction. Other nutrients were partitioned by employing Van Soest forage fiber analysis (Goering and Van Soest, 1970).

An amount of eelgrass considered sufficient for projected needs in feeding studies was harvested from Izembek Lagoon during the period 2 June to 8 June 1972. Harvesting was carried out by hand and consisted of tearing off fronds in beds exposed at low tide. The usually overcast skies and rather cold weather conditions characteristic of the area provided for a good state of preservation of the eelgrass during the week that was required to accumulate the relatively large quantity (ca. 450 kg wet weight) needed. Eelgrass was gathered into burlap bags, drained of water and shipped to the Institute of Arctic Biology by air. The entire shipment was frozen and later smaller portions were thawed and dried. Due to the large volume of dry material obtained, a hammer mill was employed for the initial grinding. Further reduction

with a burr mill was required to produce a material with the correct consistency for pelleted diet preparation.

Values accompanying means reported throughout the text are to be used as standard errors, unless otherwise noted.

Table 1. Dates, temperatures and times of experiments and number and body weights of Pacific Brant used in this study.

Experiment	Season and sex	Dates	Number	Body wt (g) mean ± SE	Test temperatures (°C)	Time period of test
Growth and Development (goslings)	Summer Male and Female	1 July - 27 Aug 1971	28	Developing goslings	outside	58 days
	Annual Male and Female	1 July 1971 - 11 Oct 1972	14	1587 ± 29	outside	15 months
Oxygen Consumption (adults)	Winter Male	1 Jan - 15 Mar 1972	33	1381 ± 23	-60 to +30	1700 - 2400 hrs
	Female		21	1409 ± 20		
	Summer Male	1 July - 15 Aug 1973	28	1615 ± 30	-50 to +30	1700 - 2400 hrs
	Female		17	1360 ± 32		
	Male and Female Winter	1 Jan - 15 Mar 1972	54	1395 ± 15	-60 to +30	1700 - 2400 hrs
	Summer	1 July - 15 Aug 1973	45	1488 ± 30	-50 to +30	1700 - 2400 hrs
Energy Balance (adults)	Summer Male	1 May - 23 July 1973	72 36	1343 ± 22	+10.8 to +18.3	5 day periods
	Female		36	1294 ± 25		
Feed Study (goslings)	Summer	13 July - 25 Aug 1972	35	Developing goslings	+7.3 to +29.0	3-6 day periods

RESULTS

Weight

The mean weight of a newly hatched, mixed-sex group of Pacific Brant was 71.3 ± 0.8 g; after approximately 24 hours the group had lost weight and averaged 60.5 ± 1.3 g. The goslings recovered this loss at 2 days of age and demonstrated rapid gains thereafter (Fig. 4). Growth rate reached a maximum (46.7 g/day) in the third week and declined in the fourth week to 17.6 g/day. Depression of the growth curve resulted from this decline in rate, but was followed by a second increase to 27.1 g/day in the fifth week (Table 2; Fig. 4). A drop by one-third to 8.6 g/day occurred in the sixth week, then by one-half to 4.3 g/day in the seventh week and reached -2.9 g/day in the eighth week (Table 2).

Body weight temporarily leveled off averaging 1145 ± 38 g in the seventh and eighth week, then continued to increase. The first depression of the weight curve resulted from a decrease in growth rate and the plateau in the seventh and eighth week resulted from both a mean weight loss and a decrease in growth rate.

Maximum weights (1837 ± 63 g) were reached by young brant in the middle of November 1971 then declined markedly until the beginning of April 1972 (1271 ± 32 g), and increased progressively until 11 October 1972 (1694 ± 38 g) (Fig. 5) when measurements were discontinued.

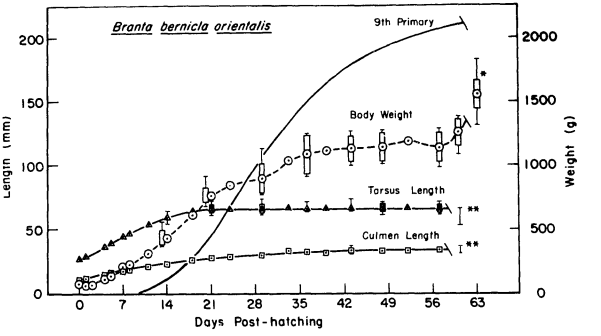
Culmen

Culmen length averaged 11.2 ± 0.2 mm upon hatching and the highest growth rate was reached during the first week (1.0 mm/day) (Fig. 4).

Table 2. Growth rates of Pacific Brant raised in captivity.

Week	Body weight (g/day)	Length (mm/day)					
		Tarsus	Culmen	Primary 9	Primary 8	Secondary 10	Rectrix 7
1	18.10	2.70	1.00				
2	33.10	2.00	0.86				
3	46.70	0.86	0.57	3.0	3.5	2.0	1.0
4	17.60	0.14	0.29	7.3	7.5	6.1	5.0
5	27.10	0.14	0.71	6.9	7.3	4.7	2.7
6	8.60	--	--	3.1	2.6	1.9	1.6
7	4.30	--	--	3.8	5.3	0.4	0.9
8	-2.90	--	--	1.4	0.3	--	--

Figure 4. Weight increase, and culmen, tarsus and 9th primary development of gosling brant. * denotes adult values; ** denotes ranges of values given by Delacour (1954). Data points are means; vertical lines are ranges. Boxes are two standard deviations.



Growth rate decreased slightly until week 5, then it increased abruptly until the end of that week when development in the long axis terminated and the culmen had reached its maximum length (34.0 ± 0.5 mm).

Depression, and subsequent recovery, of growth rate of the culmen very closely paralleled that shown by body weight and is correlated with the initial rapid rates of flight feather development (Fig. 4).

Tarsus

Immediately after hatching the length of the tarsus averaged 27.8 ± 0.3 mm and when fully developed at day 35 averaged 67.4 ± 1.1 mm. Tarsus growth was extremely rapid in the first 21 days when the mean length reached 65.2 ± 1.0 mm but had nearly stopped when flight feather growth reached high rates (Fig. 4).

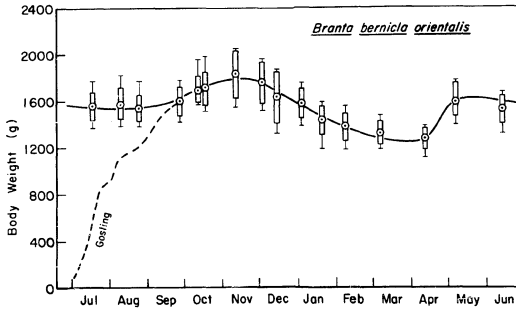
Flight Feather Development

The flight feathers of adult Pacific Brant include 10 primaries, 20 secondaries and 14 rectrices. All flight feathers were measured in this study but only the growth curves of the 8th and 9th primaries, 10th secondary and 7th rectrix are presented in Fig. 6, while mean rates of increase for these feathers are given in Table 2.

On most brant measured, rectrices were observed to emerge from pygostyle down on day 8 and remiges appeared on the wings at day 10. Primaries appeared slightly in advance (1 day) of secondaries and developed at a much faster rate, although the secondaries required less total time to complete development. All feather growth curves were regular.

In most adults, primary 9 is the longest feather and in this study

Figure 5. Weight changes of brant recorded for one year subsequent to attainment of subadult weight. Data points are means; vertical lines are ranges. Boxes are two standard deviations.



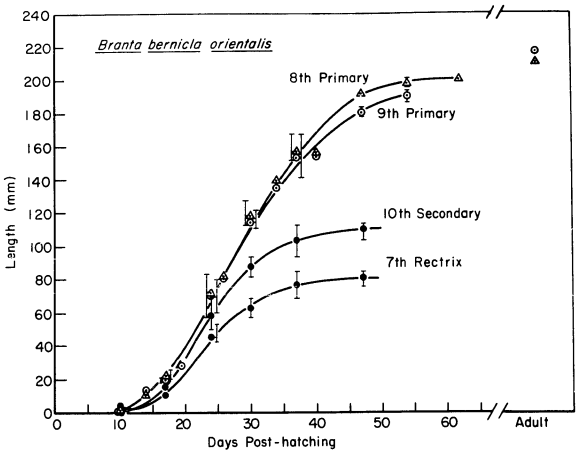
grew at its fastest rates (7.3 and 6.9 mm/day) during the second and third week of development, i.e. between the 17th and 31st days of age. The succeeding decreases in growth rate were not substantial and at the end of the first 54 days this feather averaged 190.0 ± 4.0 mm in length and was still increasing at the rate of 1.4 mm/day. When comparing the growth rates and final lengths of primaries 8 and 9, it was surprising to discover that over the major portion of the growth curve of these two feathers, primary 8 was not only longer than 9 but showed an increasingly greater rate of growth. In the sixth week of feather development, the rates of increase of the two feather were reversed and eventually the 9th primary reached greater length (Fig. 6). Average length of the fully developed 9th primary was 216.0 ± 2.6 mm (n=7).

Even in a wild population, the 8th primary is occasionally longer than the 9th. One adult collected in the last week of October at Izembek Lagoon had an 8th primary longer than the 9th at a time when full growth should have been achieved.

It was impossible to accurately follow primary growth beyond day 52 as wing exercising resulted in shattered tips, however it is expected that maximum growth of the 9th primary would be attained in 70 to 75 days after hatching.

In pattern of development, secondary 10 and rectrix 7 closely followed that of primary 9, especially in respect to rate of growth in the early period (Fig. 6). When growth of these two feathers slowed, the rate of increase of the rectrix dropped off more markedly than that

Figure 6. Flight feather growth of brant goslings. Data points are means; vertical lines are ranges. Boxes are two standard deviations.



of the secondary. Both feathers exhibited their highest rates of growth in the second week with the secondary and the rectrix reaching 6.1 and 5.0 mm/day respectively. By extrapolation, it is assumed that the secondary would reach maximum length around day 42 and the rectrix, which develops more slowly, at about day 55. Final mean lengths of these two feathers were 109.5 $\pm$ 2.7 mm for secondary 10 and 81.0 $\pm$ 3.0 mm for rectrix 7.

Figure 7 illustrates the growth pattern found for the secondaries over the first 37 days of measurements; differential growth rates favored the central group of feathers which reached a maximum at day 24 and was subsequently smoothed as all feathers attained near maximum growth simultaneously at day 37.

Oxygen Consumption Experiments

The adult body weight of male Pacific Brant is generally greater than that of the female. In contrast to this normal relationship, the mean weight of the males used in the winter tests was 1381 $\pm$ 23 g (n=33) and that of the females was slightly, but not significantly, higher (1409 $\pm$ 20 g, n=31; $P>0.05$). When tested as adults during the summer, the males averaged 1615 $\pm$ 30 g (n=28) and the females 1360 $\pm$ 32 g (n=17), a statistically significant difference ($P<0.05$) (Table 1).

Males and females in winter did not demonstrate significantly different standard metabolic rates (SMR) in the thermoneutral zone and a combined mean SMR was calculated for winter birds (Table 3, Fig. 8). On the other hand, summer rates of males within the zone of thermoneutrality were significantly greater than those of females

Figure 7. Growth pattern of secondaries over the first 37 days of brant gosling development. Data are means.

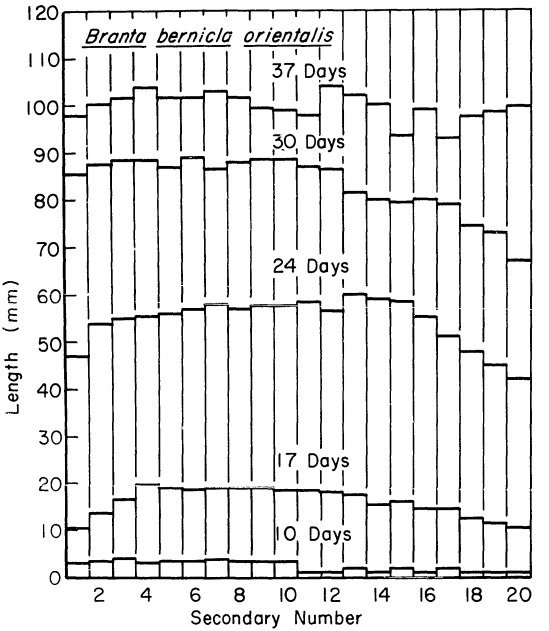


Table 3. Resting metabolic rate at thermoneutrality, linear regression equations of metabolic rate vs temperature and lower critical temperatures (T_C) of Pacific Brant measured during summer and winter.

Measurement	N	SMR at thermal neutrality (liters O_2/bird·hour±SE)	P	N	Regression equation (y=liters O_2/bird·hour) (t=T_A°C)	P (b=slope; a=elevation)	T_C(°C)
Winter							
Male	6	1.48 ± 0.10	>0.05	25	y=1.84 - 0.040(t)	b>0.05 a>0.05	8.8
Female	9	1.33 ± 0.10		18	y=1.79 - 0.038(t)		11.3
			<0.05			b>0.05 a<0.05	
Summer							
Male	9	1.13 ± 0.01	<0.05	17	y=1.18 - 0.036(t)	b>0.05 a<0.05	2.5
Female	6	0.88 ± 0.04		8	y=1.12 - 0.028(t)		8.2
			<0.05			b>0.05 a<0.05	
Combined							
Winter	15	1.39 ± 0.06	<0.05	43	y=1.81 - 0.039(t)	b<0.05 a<0.05	10.3
Summer	15	1.03 ± 0.07		25	y=1.17 - 0.033(t)		4.3
T_B Adjusted*							
Winter		---		43	y=1.72 - 0.042(t)		8.0
Summer		---		25	y=1.25 - 0.031(t)		7.0

*Regression line forced through T_B; see text.

(Table 3, Fig. 9). In order to compare combined sex winter and summer metabolic levels, a combined mean was calculated for all summer birds at these temperatures and is included in Table 3.

Through the ambient temperature (T_A) range of 0 to -60°C, which is below the lower critical temperature (T_C), the metabolic rate of winter and summer brant increased linearly with decreasing temperature according to the formulae given in Table 3 and shown graphically in Figs. 8 and 9.

Covariance analysis (Li, 1964; Snedecor, 1956) tested homogeneity of regression coefficients (slope) and homogeneity of adjusted means (elevation) of the regression lines of males and females in each season and between seasons. These tests revealed no statistically significant differences in slopes or elevations of winter males and females and the formula for metabolic increase of grouped birds in winter is presented in Table 3. Despite the seemingly wide divergence of the two summer regression lines of MR on changing T_A for males and females (Fig. 9) the "F" value obtained when subjecting the data to statistical analysis indicated that the slopes of the two lines were not statistically different. A 95 percent confidence interval was calculated which reinforced the results of the "F" test in determining homogeneity. However, the elevation of the regression line of summer males was significantly higher than that of the females. Regressions calculated for combined winter and summer data (which disregarded the difference in elevations) are presented in Table 3 and illustrated in Fig. 10.

Table 3 also gives T_C for combined winter and summer data, as

Figure 8. Standard metabolic rate of male and female winter brant in response to ambient temperature in short-term tests.

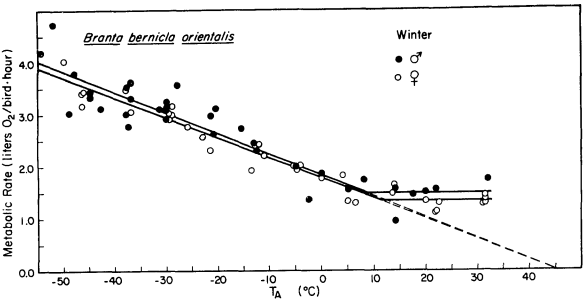


Figure 9. Standard metabolic rate of male and female summer brant in response to ambient temperature in short-term tests.

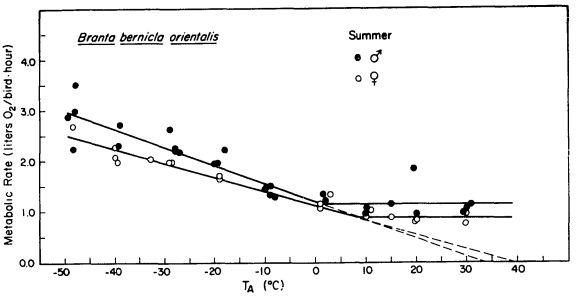
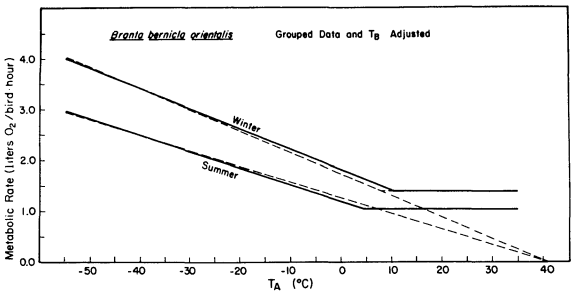


Figure 10. Standard metabolic rate of winter and summer brant in response to ambient temperature in short-term tests. Dotted lines show regressions of MR below the T_C forced through T_B.



well as for separate male and female summer data because of the statistically significant difference in elevations.

Body temperatures (T_B) were measured over 3 to 4 hours at temperatures to -50°C. It was readily apparent that body temperature was not labile under the cold stress conditions to which the birds were subjected, consequently there was no drop in T_B with the decrease in T_A. The body temperature of brant measured cloacally in this study averaged 40.9 $\pm$ 0.1°C (n=10) over the range of T_A +30 to -50°C.

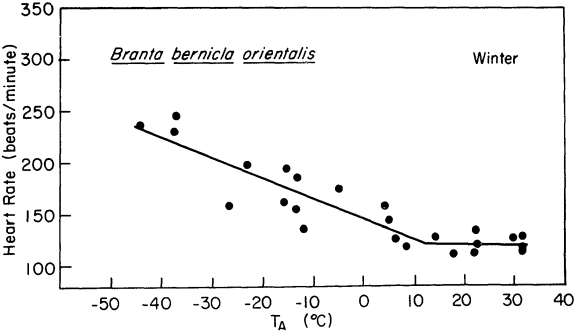
The only regression line fitted to the data for metabolism at lower T_A which extrapolated to a point close (i.e., 39.5°C) to T_B was that of summer females. Manipulation to force the regressions for grouped summer and winter metabolism through T_B resulted in a slightly steeper slope for the former and a slightly less steep slope for the latter, as well as changed T_C (Table 3; Fig. 10).

At the time that winter oxygen consumption determinations were made, some of the brant were used to provide electrocardiograms in order to establish a relationship between heart rate and metabolic rate. The mean heart rate (HR) of birds within the thermoneutral zone was 119.9 $\pm$ 3.1 beats/minute (n=9). Only the points below 0°C were used to calculate a least squares regression line of HR vs T_A. The resulting relationship of increase of HR as T_A decreased is described by the equation HR = 145.2 - 2.03(T) (Fig. 11). A T_C of +12°C was obtained from the HR vs T_A plot (Fig. 11).

Adult Energy Balance

Summer energy balance trials were carried out with adult Pacific

Figure 11. Heart rate of winter brant in response to ambient temperature in short-term tests.



Brant over the period 1 May to 23 July 1973 (Table 1); during this time 12 series of tests, each 5 days in length, were carried out with 6 birds.

The birds were exposed to naturally occurring temperatures, however the fiberglass cover of the unit containing the cages caused an elevation in cage T_A above the outside air T_A by a maximum of 2.8°C in the second trial period. Prior to the beginning of trial period 3 the roof section of the unit was covered with aluminum foil and subsequent cage T_A varied from outside T_A by +1.6 to -0.6°C. The mean temperature minimum (10.8°C) occurred in the first week, increased to the maximum (18.2°C) in the seventh, and declined to 16.3 in the final week which resulted in a 7.4°C span of T_A experienced by the birds. All mean T_A during this period were above the T_C of summer brant, as determined by this study (see above).

Reported mean weights of experimental birds are averages of measurements taken at the initiation and termination of trials; there was a statistically significant difference ($P<0.05$) between body weights of males (1343 $\pm$ 22 g; n=36) and females (1294 $\pm$ 25 g; n=36) (Table 1).

Metabolized energy (ME) was determined by the method first used by Kendeigh (1949). In this series it was also possible to directly determine existence energy, which is the equivalent of ME when the bird's weight remains relatively constant. For these trials, a weight change of up to $\pm$ 5 percent was accepted.

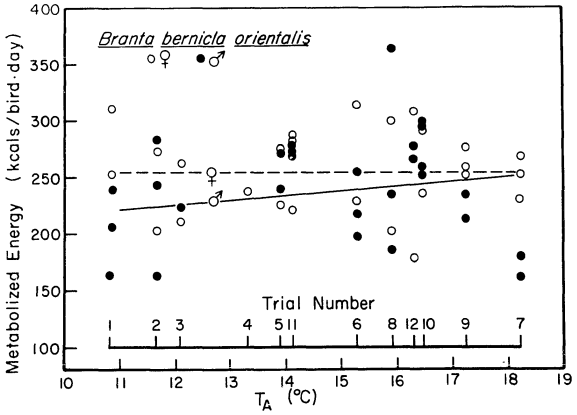
There was no statistically significant correlation between caloric

value of excrement and T_A, nor was there a statistically significant difference ($P>0.05$) in value due to sex (males: 3.880 $\pm$ 0.001, n=18; females: 3.888 $\pm$ 0.001, n=18, kcals/gram). The values utilized for calculating excretory energy (EE) were averages for individual birds and applied across the series. A mean for all birds was calculated to be 3.884 $\pm$ 0.009 kcal/gram (n=36) of excreta. Excretory energy of males (162.4 $\pm$ 5.0 kcal/bird·day, n=30) over the trial period was not significantly different ($P>0.05$) from that of females (177.4 $\pm$ 7.0 kcals/bird·day, n=26) and averaged 169 $\pm$ 4.3 kcals/bird·day (n=56). Similarly, the gross energy intake (GEI) of females (432.8 $\pm$ 13.2 kcals/bird·day, n=26) was higher, but not significantly ($P>0.05$), than that of males (399.3 $\pm$ 12.7 kcals/bird·day, n=30) and the calculated mean was 414.8 $\pm$ 9.3 kcals/bird·day (n=56). The caloric value of commercial feed used for all GEI calculations was 4.811 kcals/g (n=3) of dry weight.

Metabolized energy, which is the equivalent of existence energy as only those birds within the 5 percent weight change are included, was not significantly higher ($P>0.05$) in females (254.1 $\pm$ 7.0 kcals/bird·day, n=26) than in males (236.0 $\pm$ 9.3 kcals/bird·day, n=30), with the average being 244.9 $\pm$ 6.0 kcals/bird·day (n=56) (Fig. 12). Figure 12 also shows regressions which were calculated for male and female ME vs T_A; test for homogeneity of regression coefficients show that the two lines do not have different slopes and do not differ from zero.

On a gram body weight basis the females did show a greater ME

Figure 12. Metabolized energy (existence energy) of individually caged adult brant out-of-doors during the period May through July.



(existence energy) requirement than the males. The difference was statistically significant ($P<0.05$) and the values are 0.196 ± 0.01 ($n=26$) and 0.176 ± 0.01 kcals/gram·day ($n=30$) for females and males respectively.

Efficiency of utilization [$EOU = \frac{ME}{GEI}(100)$] of energy resources did not change during the trials for either males or females and there was no statistically significant difference ($P>0.05$) in value between the two when averaged over the entire series. The rate for males was 59.14 ± 0.7 percent ($n=30$) and for females 58.94 ± 0.6 percent ($n=26$).

Evaluation of molt in the birds involved in the energy balance trials was highly subjective, viz., "very light" for feather loss restricted to head, neck and small quantities of down to the extreme of "heavy" when large numbers of contour and/or flight feathers were found in the cage. The latter condition was recorded for 3 birds only in the first week of trials and was probably related to the stress of changed environment and restricted movements. Energy intake in week 2 indicated that the molt occurring in week 1 was not heavy enough to cause subsequent increased energy demands. For most birds intensity of molt during the trial period was "very light" to "light".

Throughout the period in which the energy balance trials were conducted, May, June and July, daylight, including civil twilight, approximates 24 hours in length. Gross activity, recorded throughout the last 11 trial periods for 3 of the 6 experimental birds, was almost entirely random over the 24-hour period each day (Figs. 13, 14 and 15). There were no marked times of onset or cessation of activity each

Figure 13. Activity record of adult brant No. 1 over the summer energy balance study period (May through July).

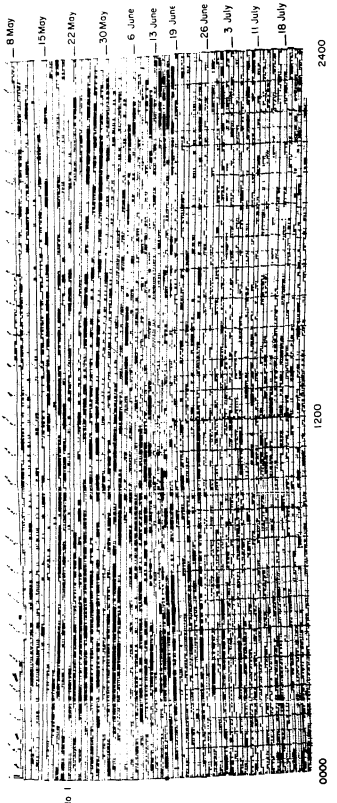


Figure 14. Activity record of adult brant No. 2a and 2b over the summer energy balance study period (May through July).

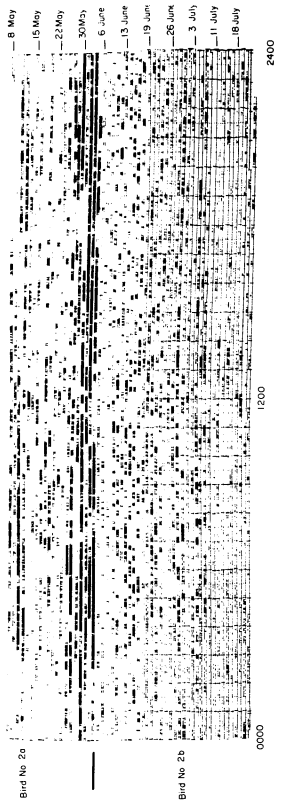
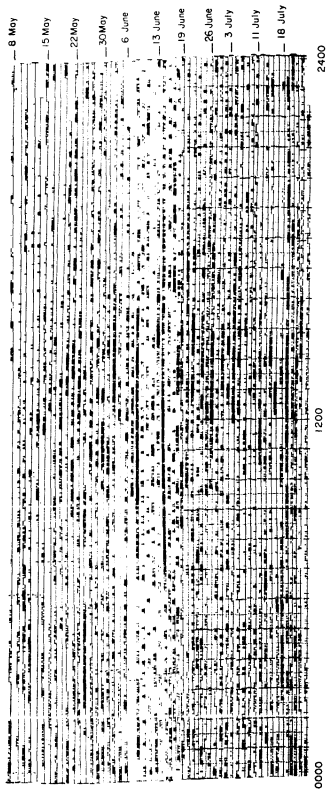


Figure 15. Activity record of adult brant No. 3 over the summer energy balance study period (May through July).



day nor were there any clearly defined periods of activity and inactivity. The former statement notwithstanding, there do appear to be some rather ill-defined similarities and differences in the individual records. One feature common to all was an early morning period of light activity, while the differences included: bird 1 (Fig. 13) showing additional periods of activity during the mid-day and late evening hours; prior to week 5, bird 2a (Fig. 14) showed the most activity in the morning hours (this changed to an intense and constant pattern of activity in the fifth week when the brant was removed from the trials) while bird 2b (Fig. 14) showed virtually equal activity throughout the day; bird 3 (Fig. 15) demonstrated a strong activity period only during mid-day. After trial period 5, the bird which had started in the 2 position was removed, due to a long-term aphagia, and another bird of the same sex was substituted for the remainder of the study.

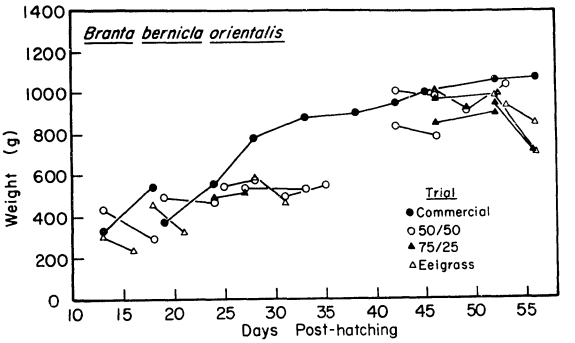
Gosling Feed Study

Summer feed studies, with young brant on commercial and eelgrass diets, were conducted over the period 13 July to 25 August 1972.

No attempt was made to modify the natural photoperiod or temperature of the birds' cage environment. Ranges and averages of T_A did not change markedly during the period of the study (43 days) as is shown by the means of 16.8°C (range, 29.0 to 9.0°C) for the last 18 days of July and 15.4°C (range, 25.6 to 7.3°C) for the first 25 days of August.

Weights of goslings graphed in Figure 16 were recorded as averages from beginnings and ends of trial periods. Only the group on commercial

Figure 16. Growth curves of gosling brant fed control and test diets in the summer.



feed demonstrated consistent weight gains; for this group of birds the growth curve appeared normal (Figs. 4 and 16). Other diets proved ineffective in producing consistent or significant weight increases in trial groups (Fig. 16). At the end of most trial periods involving diets other than commercial feed, the birds' physical condition had so deteriorated (Fig. 17) that they had to be maintained on commercial feed temporarily in order to restore their capacity for use in further trials. In the first 30 days, 3 birds on commercial feed were lost from trials, 2 due to injuries and 1 as a result of being cannibalized by a peer. Eight birds died while on other diets.

Mean caloric values of the four diets were: commercial feed, 4.802 $\pm$ 0.04 (n=5); 50/50, 4.273 $\pm$ 0.04 (n=6); 75/25, 4.017 $\pm$ 0.01 (n=2); and full eelgrass, 3.767 $\pm$ 0.01 (n=2) kcals/g dry weight. Average excrement caloric values for the above four diets were: 4.605 $\pm$ 0.09 (n=8); 4.099 $\pm$ 0.07 (n=8); 3.901 $\pm$ 0.05 (n=4); and 4.007 $\pm$ 0.05 (n=5) kcals/g dry weight, respectively. No clear trends in caloric value of excrement with time were evident within any of the groups.

Feed efficiencies (FE = unit gain in weight/unit feed consumed) were calculated for all groups to gauge the relative effectiveness of each in contributing mass to the developing birds. Mean values were: commercial, 0.19 $\pm$ 0.06 (n=8); 50/50, 0.11 $\pm$ 0.04 (n=7); 75/25, -0.15 $\pm$ 0.10 (n=4); and full eelgrass, -1.99 $\pm$ 0.70 (n=4). The difference between FE of commercial feed and 50/50 and between 75/25 and full eelgrass were not significant ($P>0.05$); there was a statistically

Figure 17. Brant gosling from test diet group showing poor feather development and appearance.

significant difference ($P<0.05$) between the FE of the 50/50 and 75/25 diets. Least squares analysis of data for commercial feed and 50/50 diets, the 2 in which there appeared to be trends (Table 4), revealed that with the 50/50 diet no change in FE occurred with time (slope not different from 0) and that with the commercial feed, the two parameters are significantly (negatively) correlated. When the 50/50 diet value for day 3 (FE = 0.31) was excluded a significant ($P<0.05$) positive correlation between day and FE value resulted; regression equations of FE vs time for both diets are given in Table 4.

Efficiency of utilization (EOU), a more sensitive and precise measure of the birds' ability to utilize a food resource, was calculated for all groups; percent averages were 60.3 ± 0.01 (n=8) for commercial, 33.5 ± 0.02 (n=7) for 50/50, 14.4 ± 0.02 (n=4) for 75/25, and -39.4 ± 0.14 (n=4) for full eelgrass. Statistically significant differences ($P<0.05$) in EOU were found between all groups. Least squares analysis of EOU data for the 50/50 diet, both with and without the results for day 3 (EOU = 41.7 percent), showed no significant ($P>0.05$) change with time (slope not different from 0). Efficiency of utilization data for commercial feed showed a decrease with time and the relationship was statistically significant ($P<0.05$); the regression equation describing this relationship is given in Table 4.

Covariance analysis of EOU and FE of both commercial feed and 50/50 diets were carried out. No statistically significant difference ($P>0.05$) was found between the EOU regression coefficients or between the FE adjusted means, however, a statistically significant difference

Table 4. Efficiency of utilization (EOU) and feed efficiency (FE) of gosling Pacific Brant consuming commercial ration and mixtures of commercial ration with eelgrass diets.

Day of Study+	Commerical diet		50/50 diet		75/25 diet		Eelgrass diet	
	EOU	FE	EOU	FE	EOU	FE	EOU	FE
2							-1.0	-1.65
3	65.7	0.46	41.7	0.31				
7							-57.8	-0.64
9	61.9	0.37	26.3	0.04				
13	64.9	0.34			16.7	-0.03		
14			33.0	0.01				
17			38.9	-0.01			-61.0	-4.11
18	60.8	0.16						
20			36.2	0.10				
23	57.1	0.04						
27	59.8	0.11						
31			25.5	0.14				
35					16.1	-0.49		
36	62.7	0.12			17.4	-0.26		
38			32.9	0.15				
41	49.6 (a)	-0.05 (b)	(c)	(d)	7.3	-0.34	-33.3	-1.60

(a) - Y EOU = 66.3 - 0.19t
(b) - Y FE = 0.45 - 0.01t
(c) - Y EOU = 32.9 - 0.03t*
(d) - Y FE = 0.041 + 0.01t*

+Days are mid points of successive trials.
*Denotes regression calculated without day 3 data.

($P<0.05$) was found between EOU adjusted means and the FE regression coefficients. The limited data available for the other two diets did not allow for meaningful covariance or regression analysis (Table 4).

Eelgrass Collections

Results of investigations of seasonal variation in chemical composition and caloric value of eelgrass are presented in Table 5.

Protein, total lipids and lignin components were observed to vary only slightly throughout the collection period. Protein values ranged from a low of 9.8 to a high of 13.7 percent (mean, 11.3 ± 0.2), however the values fluctuated irregularly and a difference between sample sites was as great as 1.7 percent in a single collection. All lipid values were lower than 1 percent, most were well below 0.5 and averaged 0.33 ± 0.03 percent; differences between sample sites for a given collection were as much as two- or three-fold. Lignin values were essentially constant over the series, the mean was 4.8 ± 0.2 percent and values ranged from 3 to 6 percent with the greatest difference between sites being 2 percent.

The soluble carbohydrate fraction showed an increase in the beginning of the period (between 15 May and 2 June), peaked in early July, then declined slowly until it made a substantial drop in the late season (between October 3 and November 19). Soluble carbohydrates averaged 32.4 ± 1.4 over the collection period and at various times made up 25 to 35 percent of the total for all constituents.

Cellulose, which was relatively high (approximately 30 percent) for the first two collections, attained a seasonal low of 15 percent in early June. Subsequent values tended to increase until early July

Table 5. Seasonal (15 April -- 19 November) changes in chemical composition expressed as percent of dry matter and caloric value of eelgrass (Zostera marina) from Izembek Lagoon, Alaska.

Collection date and site	Soluble carbohydrates	Fiber		Protein (N-6.25)	Total lipid	Ash	Caloric value (kcal/g organic matter)
		Lignin	Cellulose				
4-16 A		6	28	10.3	0.27		
B		6	30	11.3	0.34		
5-15 A	25.3	6	28	11.8	0.19	28.7	4.19
B	23.7	6	32	12.4	0.38	35.5	4.14
6-2 A	34.2	4	15	10.7	0.27	35.8	4.11
B	33.1	3	15	12.1	0.25	36.5	4.15
6-18 A		5	18	12.0	0.23		
B		4	20	12.1	0.31		
6-30 A	33.2	5	22	11.4	0.70	27.7	4.11
B	36.9	5	17	12.8	0.43	27.9	4.06
7-6 A		4	19	11.2	0.31		
B		3	19	11.7	0.22		
8-3 A	37.4	5	25	10.7	0.33	21.6	4.15
B	36.8	4	26	9.0	0.48	23.7	4.13
8-17 A		5	18	10.7	0.14		
B		5	21	10.4	0.35		
9-3 A	35.7	6	21	9.8	0.63	26.9	3.95
B	36.4	6	20	10.3	0.62	26.7	4.01
9-15 A		4	18	10.9	0.24		
B		5	18	11.1	0.38		
10-3 A	34.8	4	21	10.7	0.22	29.3	3.90
B	35.5	6	17	10.2	0.26	31.0	3.91
11-2 A		4	21	13.7	0.21		
B		4	19	13.3	0.19		
11-19 A	27.5	5	22	12.0	0.15	33.2	3.92
B	22.7	5	22	11.0	0.48	36.8	3.85

Regression equation is $y = 4.41 - 0.05\ t$ (y = kcals/g of ash free dry matter, t = time in months).

when they reached approximately 25 percent, thereafter a drop occurred to a level of about 20 percent which was maintained throughout the balance of the collection period. The average value of cellulose for the series was 21.2 $\pm$ 0.9 percent.

Ash values exhibited somewhat the same pattern as soluble carbohydrates except that the trend was from high to low values from the beginning of the collections to early July, and then a steady increase through November; mean value for all ash samples was 30.1 $\pm$ 1.3 percent.

Caloric value of eelgrass samples showed a moderate decline over the sampling period; the range was from 4.170 to 3.890 kcals/g of ash free dry matter, given as averages of the second and last collections respectively. Least squares regression analysis showed that the change of caloric value with time was significantly different from zero ($P<0.05$) (Table 5). Average caloric value of eelgrass over the series was 4.042 $\pm$ 0.03 kcals/g.

DISCUSSION

Growth and Development

In 1957, Weller expressed concern about the paucity of published information on growth, weight and plumage development of waterfowl despite their long history of culture by man. In the last seventeen years the situation has improved somewhat. The modest growth of available information has however resulted almost exclusively from studies on birds from the subfamily Anatinae (ducks) and in comparison very little progress has been made with the Anserinae (swans, geese and whistling ducks). Consequently comparison of the growth and development of brant to other Anatidae have been made almost entirely with ducks rather than to other geese with which they are more closely allied.

The growth and development study reported here for captive Pacific Brant had as its primary purpose the establishment of a set of data, for birds on a high plane of nutrition, which could be used as a set of norms for evaluating performance of goslings in feeding trials. The study provides a preliminary picture of brant development which can be applied to, or modified for, field investigation.

The immediate post-hatching weight loss of Pacific Brant found in this study also occurs in other species of waterfowl (Kear, 1965; Smart, 1965; Cain, 1970). Post-hatching weight loss results from drying of embryonic fluids and utilization of yolk nutrients during and after hatching (Kear, 1965). Kear (1965) also suggests an increased metabolism

of young during early post-hatching resulting from mobilization of yolk reserves for storage in other organs, primarily the liver, which contributes to weight loss over this period.

Recovery of hatching weight is rapid, e.g., the Pacific Brant in this study accomplished this in 2 days, the large Great Basin Canada Geese (Branta canadensis moffitti), studied by Yocum and Harris (1966), required 3 days, and the Ruddy Duck (Oxyura jamaicensis) (Siegfried, 1973) required 4 days, the longest period noted for any waterfowl.

Geese in this study experienced a decrease in rate of gain commencing about day 23, which corresponded with the beginning of the period of greatest remige growth. This pattern has been found in captive reared Redhead (Aythya americana) (Weller, 1957), Ruddy Ducks (Siegfried, 1973), 5 species of European divers and dabblers (Veselovsky, 1953), Cape Barren Geese (Cereopsis novaehollandiae), which are ducks of the tribe Tadornini (Delacour and Mayr, 1945), and Lesser Snow Geese (Anser caerulescens caerulescens) by Barry (1967). Dzubin (1959), working with free-living Canvasbacks (Aythya valisineria), and Schneider (1965), studying free-living Mallards (Anas platyrhynchos), Canvasbacks, and Lesser Scaup (Aythya affinis), in interior Alaska, did not find this pattern. Weight curves described by Hanson (1958) for Giant Canada Geese (B. c. maxima) and Yocum and Harris (1966) for Great Basin Canada Geese also do not indicate this decrease in rate of weight gain during primary development. Decrease in rate of weight gain in Pacific Brant did not result in a plateau in the weight curve.

A second decrease in rate of weight gain in the brant, which

commenced about day 37, did result in a plateau as most birds lost weight initially and then stabilized over a 19 day period. A weight loss occurring at that time, attributed to energy cost of first flight, has been recorded in almost all similar studies. Body weights in some species have been noted to drop markedly during pre-fledging, as is illustrated in the weight curve for captive Giant Canada Geese (Hanson, 1958) and for wild Lesser Snow Geese (Barry, 1967). An abundant food supply and restricted area for activity for the brant may have prevented this weight loss. A pre-fledging weight decrease was not clearly apparent in young Great Basin Canada Geese which were hand raised (Yocum and Harris, 1966).

Apparently there are no published yearly weight curves for wild Pacific Brant; therefore the degree to which the yearly weight curve found for captive brant in this study represents that of free-living birds is unknown. It is assumed that changing sex or age structure through differential mortality of males or females or "missed" breeding seasons, a not uncommon occurrence with brant, would influence the yearly weight curve of the wild population. The present data show two periods of decrease in weight (winter and summer) each of which is separated from the other by a period of increase (Fig. 5) the greatest of which occurs in the late fall. The two periods of weight decrease, which are manifestations of negative energy balance, correspond generally to those found for Interior Canada Geese (B. c. interior) (Williams, 1965). Body weights of brant have been determined by various

investigators at specific times of the year only, the bulk of the data has been accumulated on moulting birds. A weight curve for Pacific Brant during the reproductive season as given by Barry (1967) does not generally correspond to present data over the same time period (April through September). Further, Barry's data points represent a sample size of three or less. Einarson (1965) reported weights obtained for summer brant on the Yukon-Kuskokwim Delta 1332 g (n=150). This average weight (1332 g) should represent a near minimum weight for summer brant as weight losses of from 10 to 15 percent have been documented for geese during the summer non-flying moult period (Hanson, 1962) and, although not specifically stated, Einarson's (1965) weight data appear to have been obtained from flightless non-breeding geese. Mean summer weight of brant from this study was well below (160 g) that calculated from Einarson's (1965) data. This difference may be explained on the basis of time of moult as considerable differences in mean values can be expected as the moult progresses (Matthews and Campbell, 1969). Weights for July-August moulting of Pacific Brant on the Yukon Delta show that there is a considerable mean weight fluctuation over the year (males: 1264 g, n=277; females:1080 g, n=285) and for February-March birds on the British Columbia coast (male: 1450 g, n=189; females: 1300, n=181) (Hansen and Nelson, 1957). In this study the winter-summer weight relationship found by Hansen and Nelson (1957) was reversed.

Four brant, 2 adults and 2 immatures, collected from Izembek Lagoon in late October averaged 1781 g; the largest weighed 2110 g. This small sample provides some evidence for a yearly weight peak for wild Pacific

Brant occurring, as the curve for captive brant indicates, immediately prior to southward migration in late October or early November. Larger and more frequent samples must be accumulated before a representative yearly weight curve can be constructed for the wild Pacific Brant population.

In the Pacific Brant the tarsus grows faster and completes development more quickly than the culmen, as is the case with most other birds (Huggins, 1940). Canvasbacks are reported to be an exception among waterfowl, as the culmen shows more rapid development than the tarsus over most of the growth curve (Dzubin, 1959); however even with these birds the curve for tarsus growth flattens before that of the culmen.

In this study on Pacific Brant, culmen length was assumed to have reached a maximum about day 43 as the 3 succeeding measurements did not indicate a continued increase; the mean length of 34.0 mm agreed well with Delacour's (1954) range of 32-37 mm for wild birds of the same subspecies. Hanson (1951) has shown for Canada Geese that the culmen lengths of adults were no longer than those of immatures in their first year of life. In contrast, Matthews and Campbell (1969) found a statistically significant increase in culmen length for male Greylag Geese (Anser anser) over the first winter; in females the increase just failed to reach statistical significance. Preliminary evidence in data on Spectacled Eider (Somateria fischeri) and Cackling Canada Geese (B. c. minima) indicates that a "shrinkage" apparently occurs in the culmen (as well as tarsus) as lengths of these body parts in adults is less than that of immatures (C. Dau and P. Mikkelson, pers.

comm.). As no measurements were taken on birds in this study after day 57, a subsequent decrease in mean length would not have been noted.

Tarsi of the captive Pacific Brant developed rapidly and had essentially stopped growing by day 21. As with the culmen, rate of tarsus growth was the greatest during the first week of life. Unlike weight increase and culmen growth the tarsus exhibited no second increase in growth rate. Delacour (1954) gives a range of 53-66 mm for tarsal measurements of Pacific Brant, which is shorter than that found in the captive group (62-72 mm). It is not known to what extent Delacour's values were influenced by sex ratio. There were sex related differences in tarsal length and weights of the captive brant, but not in culmen length.

There appears to be a continuum of rate of tarsal development among waterfowl, which is shown by the following examples. Siegfried (1973) found that the culmen and tarsus development from hatching of Ruddy Ducks (tribe Oxyurini) was slower than that in other divers (Aythyini). However, at the time of hatching the tarsus was about 60 percent of adult length. The middle toe of the Ruddy Duck was found to have a more rapid growth rate than the tarsus, which was presumed to be an adaptation for diving as it results in a realtively large foot at an early age. The Aythini (Dzubin, 1959; Kear, 1970; Weller, 1957) have tarsi which develop more swiftly than that of the Ruddy Duck and reach full development in 6 to 8 weeks. Data on Cape Barren Geese indicate a tarsus and culmen development pattern very much like that of the Aythyini (Veselovsky, 1973). Pengelly and Kear (1970) state that rapid leg development in many waterfowl is presumably an adaptation to life

on rapidly flowing water. Kear (1970) compared relative growth rates of the ducklings and found that dabblers, although smaller at hatching, develop at greater rates than divers. It is assumed that a proportional growth takes place with the tarsus in dabblers and maximum length is obtained sooner than the 6 to 8 weeks required for divers; the rapid development of the tarsus of dabblers is presumably an adaptation to their more terrestrial way of life.

In comparison Canada Geese, weighing some 2700 to 3200 g when fully grown, completed tarsus growth by the 7th week of life (Yocum and Harris, 1966). Considering body size and when compared with the other groups of waterfowl, time of completion of tarsus development in Canada Geese was as extremely abbreviated as it was for Pacific Brant in this study (21 days).

Feathers grow at rates which are dependent upon species, age, feeding habits, physical condition, time of year and time of day (Welty, 1962).

Plumage growth and development studies on waterfowl have, for the most part, been management oriented, i.e., designed to contribute to the facilitation of ageing and/or sexing of birds in the field. Therefore, much of the descriptive work involves general appearances, and intra- or inter-specimen comparisons of various growth parameters. Studies which have reported flight feather measurements which are comparable to this study are relatively few in number.

A notable difference found in sequence of feathering between captive Pacific Brant and other waterfowl was that in the diving ducks (Redhead,

Canvasback) development of the secondaries preceded that of the primaries (Weller, 1957). The pattern observed and illustrated graphically in Cape Barren Geese, by Veselovsky (1973), appears to be similar to that recorded for the 2 Aythya species. The reverse was true in this study; the primaries were markedly dominant in their development and all could be counted on day 10, whereas it was 3 to 5 days later before measurements could be taken on all secondaries. Other feather growth phenomena such as the differential growth of "outer" and "inner" rectrices and the length reversal of primaries 8 and 9 during development have hitherto been unreported. It may be that these patterns are unique in geese, in brant, or to this study.

Early flight is of course strongly dependent upon a rapid rate of flight feather (remige) development, and the age at which flight is attained decreases from divers to dabblers, and then to geese (Weller, 1957; Barry, 1967). The age of first flight relationship between geese and other waterfowl is perhaps not so obvious due to the great range in size of the geese, but development and flight readiness proceed rapidly as is shown by growth of body parts and feathers. Soper (1930) observed Blue (Snow) Geese (Anser caerulescens caerulescens) in the Foxe River Basin of Baffin Island which had hatched in mid-July making flights "a little more than a month later", while Cooch (1953) has given 5 weeks for first flight in the same subspecies. Barry (1967) provided a weight curve for Snow Geese from the Anderson River Delta, N.W.T. which, if interpreted correctly using the pre-fledging drop in weight as a guide, indicates an approximate first flight age of about 40 days. Barry (1967)

also notes that growth and development of White-fronted Geese (Anser albifrons) parallels that of the neighboring Snow Geese with hatching and flying times not distinguishably different. Mikkelson (1973) on the other hand states that the larger White-fronted Geese fledge at 55 to 65 days on the Yukon-Kuskokwim Delta and that Emperor Geese (Anser canagicus) were not greatly in advance of the former with fledging ages of 50 to 60 days. This rather large discrepancy in fledging ages of White-fronted Geese might be explained on the basis of an increase in rate of plumage development with increasing latitude. However this thesis is not supported by Schneider's (1967) comparison of results of his own work in Alaska on ducks with results obtained on the same species at lower latitudes.

The Canada Geese comprise at least 12 races (subspecies) (Delacour, 1954) which range in size from B. c. minima (Cackling Goose) of some 1.1 kg to B. c. maxima which has been known to reach more than 9.0 kg. The smaller of the two races attains flight in 40 to 46 days (Mikkelson, 1973) and the largest in just over 10 weeks (Hanson, 1958). Ages of first flight for some of the more intermediate sized Canada Geese are 49 to 56 days for Great Basin Canada Geese (Moffitt, 1931) and approximately 63 days for Interior Canada Geese (Hanson, 1965). When the ages given above are compared with the 60 and 70 day average ages calculated for diving ducks (Weller, 1957) it can be seen that there is an acceleration of flight readiness in geese despite greater size.

Brant appear to have the most accelerated plumage development among the geese. Einarson (1965) reports the age for first flight of Pacific

Brant as seven weeks while Barry (1967) reports 40 to 45 days and Mikkelson (1973) ca. 40 days. Mikkelson (1973) notes that on his study area in coastal Alaska brant grew faster and gained flight earlier than similar sized Cackling Geese.

There are undoubtedly many factors which determine age of first flight in birds, however one of the most important must be critical wing area. Critical wing area is probably best indicated by primary development at time of flight and expressed as a percentage of total growth. Total growth, or length, of primaries increases in Canada Geese from the first through the third molt (Hanson, 1958). Studies in which total growth was found to occur or be necessary before flight were not found, generally waterfowl fledge considerably before primary growth ceases (Weller, 1957). Percent of total primary growth at first flight has not been determined in the field for any waterfowl, and few authors give an estimate for captive birds. This study does not indicate at what age the birds were able to sustain flight as they were closely confined, but an entry in the record indicates an ability to rise vertically a short distance and make an abbreviated flight at 35 days of age. According to the primary growth curve determined in this study, the 35 day-old captive birds and Mikkelson's (1973) 40 day-old fledged brant had completed 68 and 80 percent of their total growth, respectively.

Oxygen Consumption

The body weights of male Pacific Brant (1615 g) used in the summer oxygen consumption trials were greater than the females (1360 g) (Table 1). In the winter trials however, male body weights (1381 g) were somewhat,

but not significantly, lighter than those of the female birds (1409 g). The reversal of weight relationship in winter may be a result of the immature (subadult) status of the birds when used in the trials, i.e. before a sex dependent weight differentiation had occurred.

The mean body temperature (T_B) recorded for brant in this study (40.9°C) does not differ appreciably from that given for domestic geese (40.8°C) by Benedict and Lee (1937) or that reported for 2 brant by Irving and Krog (1954) (40.5°C) for measurements taken at T_A of -23 and -24°C. Irving and Krog's (1954) T_B measurements (range, 39-42°C) were taken during brief, physical restraint of the birds, while those of this study (range, 40.5-41.5°C) were obtained from cloacally inserted thermocouples (6 to 7 cm) over a period of 1 to 2 hours at a wide range of T_A.

Despite a reversal of the usual weight relationship of male and female brant, the mean resting metabolic rate of males in winter at thermoneutrality was higher on a per bird basis, but not significantly, than that of females tested during the same period. The larger summer acclimatized males had a significantly higher average metabolic rate than that of the lighter females. There was a highly significant difference between thermoneutral resting rates of winter and summer Pacific Brant. The combined weight specific rate at thermoneutrality in this study was higher in winter and lower in summer than those reported by Irving et al. (1955). Irving et al. (1955), working with a single brant, found no marked difference between the summer and winter basal metabolic rates

(BMR). Although not having absolute values, the data of Irving et al. (1959) was presented in a form such that the BMR was given as 100 and thus readily comparable to other data; from it a temperature of -31°C is obtained for the point at which the brant doubled metabolic rate during both winter and summer (the regression formulae would therefore be essentially the same for metabolism below T_C in summer and winter). The reported T_C is the same for both seasons and both regression lines extrapolate to T_B. By assigning metabolic rates at thermoneutrality obtained in this study the value of 100, it was determined that females and males in summer doubled their rates at -24.5 and -31°C, respectively; the temperature at which doubling of the MR for both groups occurred was -28°C. Using this combined rate for male and female winter birds the doubling of O_2 consumption was found to occur at -24°C. The difference between the temperatures at which doubling of the metabolic rate occurred in winter in this study and that of Irving et al. (1955) appears to be related to the flatter slope of the regression line determined in the latter.

Irving et al. (1955) found a lower T_C of 6°C for both winter and summer acclimatized brant. In this study, the winter lower T_C for both males and females was 10.3°C. Lower critical temperatures of summer males and females in this study were 2.5 and 8.2°C respectively.

The seasonal relationship in rate is not altered by expressing the metabolic rates on a gram body weight basis. In fact, the difference is magnified because experimental birds used in the summer were heavier

(1488 g) than those used in the winter tests (1395 g) (Table 1). When calculated on a per gram body weight basis, the rate at thermal neutrality for summer birds was 0.69 $\pm$ 0.03 and for winter birds 1.01 $\pm$ 0.04 $cc O_2/g \cdot hr$; linear increase of metabolism for the 2 groups below the T_c are described by the formulae $y = 1.30 - 0.028(t)$ and $y = 0.79 - 0.022(t)$, for winter and summer respectively (y is expressed in $cc O_2/g \cdot hr$, t in °C).

Table 6 shows that the male and female Pacific Brant combined winter standard metabolic rate (SMR), measured in the dark and at thermoneutrality, was higher than the rates predicted on the basis of body weight by equations given by Lasiewski and Dawson (1967), Aschoff and Pohl (1970), and Dolnik (1974). The SMR of summer males was essentially the same as that predicted by Aschoff and Pohl (1970) and Dolnik (1974), but was 15 percent higher than that predicted by Lasiewski and Dawson (1967). The SMR for summer females agreed well with Lasiewski and Dawson's (1967) predicted rate, but was below those of Aschoff and Pohl (1970) and Dolnik (1974). The active (α) time formula of Aschoff and Pohl (1970) for SMR was used for their predicted rates given above as the birds when tested were judged to be in an active period (this study; C. Dau, pers. comm.; Hochbaum, 1955).

A significantly higher winter than summer metabolic rate whether expressed on a per bird or per gram body weight basis (approximately 50 percent higher than that predicted by various standard rate formulae at thermoneutrality) is not readily explained. The annual program for

Table 6. Measured and predicted rates of metabolism at thermoneutrality and of thermal conductance below thermoneutrality for Pacific Brant.

	Mean body wt (g)[1]	SMR (kcals/bird·day)				EMR (kcals/bird·day)			Thermal conductance (C) ($cc O_2$/g·hr·°C)	
		This study	Lasiewski and Dawson (1969)[2]	Aschoff and Pohl (1970)[3]	Dolnik (1974)[4]	This study	Kendeigh (1970)[5]	Dolnik (1974)[6]	This study	Lasiewski et al. (1967)
Winter										
Male	1381	166.94	98.88	115.14	117.69	--	126.47	185.55	0.0290	0.0215
Female	1409	150.02	100.33	116.84	119.24	--	128.40	188.03	0.0270	0.0213
Summer										
Male	1615	127.46	110.73	129.06	130.35	236.0	142.33	205.78	0.0223	0.0199
Female	1360	99.26	97.79	113.86	116.52	254.10	125.02	183.68	0.0206	0.0217
Male and Female										
Winter	1395	156.79	99.61	115.95	118.47	--	127.44	186.80	0.0280	0.0214
Summer	1488	116.18	104.37	121.58	123.56	244.9	133.80	194.94	0.0222	0.0207

[1]Data from Table 1.

Formulae for predicting (a) SMR, (b) EMR and (c) thermal conductance on the basis of body weight (W):

a: [2]$\log M = \log 78.3 + 0.723 \log W$ (W in kg)

[3]$\log M = \log 91.0 + 0.729 \log W$ (W in kg) for α time

[4]$\log M = \log 95.32 + 0.653 \log W$ (W in kg)

B: [5]$\log M = -0.2673 + 0.7545 \log W$ (W in g)

[6]$\log M = \log 149.9 + 0.661 \log W$ (W in kg)

C: [7]$\log C = \log 0.848 - 0.508 \log W$ (W in g)

Pacific Brant is such that temperature extremes are encountered only briefly and irregularly; atmospheric and/or oceanic influences in both northern and southern extremes of the range exert moderating effects which provide a relatively constant thermal environment. The coldest temperatures are encountered in summer while the birds are on their arctic and subarctic breeding ground, therefore one would expect greater insulation and lower MR in summer than in winter in wild birds. In this study, the average temperature to which the experimental birds were exposed in summer (15°C) did not differ greatly from the winter average temperature (9.5°C). If the birds respond metabolically according to their immediate prior thermal history, MR in winter and summer should have been approximately the same. The elevated MR of winter birds may be explained as follows. First, circannual rhythms have been described for molt, breeding cycles and nightly unrest in passerines (Berthold et al., 1972). Birds which in their annual programs are normally exposed to colder summer temperatures might be expected to develop greater insulation than in winter regardless of an experimental acclimatization temperature. Therefore, in winter, birds having less insulation (greater C) would have higher MR at comparable T_A, as has been demonstrated in this study. This hypothesis assumes that the acclimatization temperature is not as significant a factor in control of development of insulation as is a circannual oscillator. Although no such endogenously operating circannual rhythm of plumage density or total insulation has as yet been demonstrated, this does not preclude

the possibility that such oscillators occur. Further experimental work in this area is necessary in order to resolve this question.

Secondly, age differences of the winter (9 mos.) and summer brant (2 yrs.) may have been a factor in producing unexpectedly high winter rates. The juvenile brant with lower average body weights had significantly higher MR on a gram body weight basis. Brant, as other geese, generally do not mature sexually until their third year of life. They continue to to increase in weight in the first few years of life and different age groups may have markedly different MR, as has been demonstrated for other animals (Brody, 1945). The latter hypothesis should be tested by conducting winter trials with adult birds under experimental conditions similar to those under which the 9 month old birds were previously tested.

Regression lines of metabolic rate below T_C calculated for summer and winter Pacific Brant did not extrapolate to T_B according to the Scholander model for heat loss based on Newtonian cooling (Scholander et al., 1950), therefore values presented here as thermal conductance (C) do not necessarily represent total thermal conductance (C_t) (see Pohl, 1969; Pohl and West, 1972). In this study, it has been assumed that C is constant at all temperatures below thermoneutrality (Herreid and Kessel, 1967). Values of C obtained from regression coefficients of metabolic rates of brant below the T_C were 7 percent higher for combined sex summer (0.0222 $cc O_2/g \cdot hr \cdot °C$) and 31 percent higher for combined sex winter data (0.0280 $cc O_2/g \cdot hr \cdot °C$) than those predicted by the equation $C = 0.848W^{-0.508}$ (Lasiewski et al., 1967). The greater

thermal conductance is a concommitant of the increased metabolic level found for winter brant in this study. Thermal conductance values predicted for brant studied by Irving (1955) using the equation of Lasiewski et al. (1967) were 0.0238 and 0.0234 $cc O_2/g \cdot hr \cdot °C$ for summer and winter, respectively, and are comparable to those found in this study. Minimum thermal conductance values for brant are lower than all others found in the literature except that of 0.0104 $cc O_2/g \cdot hr \cdot °C$ for the Snowy Owl (Nyctea scandiaca) (Gessaman, 1972). Recent work with the Emperor Goose (Anser canagicus) also reveals a lower conductance (0.0142 $cc O_2/g \cdot hr \cdot °C$) than that found for the brant (Morehouse and West, unpubl.). Low thermal conductance (high insulation) values may be characteristic of waterfowl. Due to a higher specific heat, water has a greater capacity for heat transfer than does air. Thus for a group such as the waterfowl, which are highly aquatic, a low thermal conductance would have great adaptive significance. Thermal conductance values calculated for Hartung's (1967) metabolism data on Mallards and Black Ducks (Anas rubripes) were both approximately 0.0250 $cc O_2/g \cdot hr \cdot °C$. Thermal conductance values for other northern resident or seasonally resident birds are generally higher. The C value of a Mew Gull (Larus canus), a casually aquatic species, determined by cooling rates of carcasses was 0.19 $cc O_2/g \cdot hr \cdot °C$; that of the more terrestrial Sandhill Crane (Grus canadensis) obtained in the same way was lower at 0.09 $cc O_2/g \cdot hr \cdot °C$ (Herreid and Kessel, 1967). West (1972) reported values of 0.12 and 0.18 $cc O_2/g \cdot hr \cdot °C$ for winter Willow Ptarmigan (Lagopus lagopus) and

Rock Ptarmigan (Lagopus mutus), respectively, which were obtained from metabolism data. Both of the ptarmigan are winter residents but are found upland. Summer thermal conductance for the coast inhabiting Northwestern Crow (Corvus caurinus) is somewhat intermediate to all of the above (0.051 $cc0_2/g \cdot hr \cdot °C$) (Irving et al., 1955).

Heart Rate

The relationship of heart rate at rest to T_A (Fig. 11) measured in winter acclimatized Pacific Brant is similar to that of SMR vs T_A in both summer and winter (Figs. 8 and 9). A cardiac zone of neutrality shown in this study is characteristic of birds with relatively large hearts (Brush, 1966) and has been reported by Drent and Stonehouse (1971) for the Peruvian Penguin (Spheniscus humboldt), Hudson and Brush (1964) for the Mourning Dove (Zenaidura macroura) and Coulombe (1970) for the Burrowing Owl (Speotyto cunicularia).

The T_C of 12°C for brant shown in the plot of T_A vs HR is about 2°C above the T_C of metabolic rate during winter. Lower T_C for cardiac and thermal neutral zones have been shown to differ slightly by Drent and Stonehouse (1971) in penguins and Hudson and Brush (1964) in doves. A 10°C wide thermal neutral zone and lack of a zone of cardiac neutrality in California Quail (Lophortyx californicus) (Hudson and Brush, 1964) demonstrates that the two T_C need not be closely associated. Separate cardiac and thermal zones of neutrality may also occur in mammals (Pigmy Possum, Cercaertus nanus; Bartholomew and Hudson, 1962).

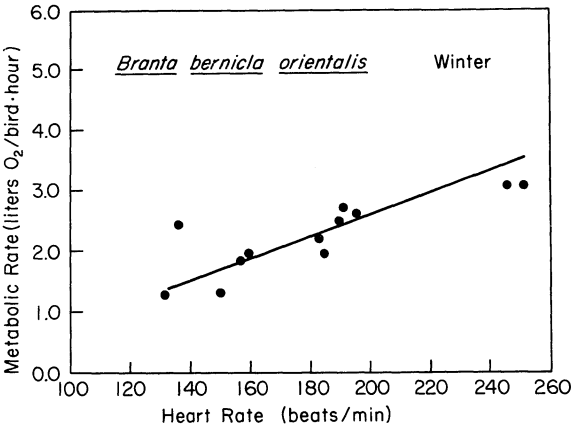
The relationship between heart rate and metabolic rate has not been

specifically shown for birds, however it can be inferred from data showing that MR is correlated with T_A and HR is correlated with T_A, that therefore MR is correlated with HR (Johnson and Gessaman, 1973). Owen (1969) stated this concept in the following manner: "since both heart rate and existence metabolism are linearly correlated with temperature, they are linearly related to each other". This applies to standard metabolism as well.

A linear correlation has previously been demonstrated between T_A and each of the other two physiological parameters (SMR and HR) measured in this study. Figure 18 shows the linearity of the relationship of heart rate and metabolism below the winter T_C of captive brant. The least squares regression line calculated for HR vs MR is described by the equation MR = -0.09 + 0.013 (HR) ($r = 0.83$; $F = 21.0$, df 1, 10; $P<0.05$).

The relationship of HR vs MR obtained in the winter series probably has limited predictive power outside of this study, not only because it was established for standard rates of metabolism but also because the HR vs MR relationship may change seasonally as has been found for the Burrowing Owl (Coulombe, 1970). Caution must be exercised when extrapolating to a single individual as HR is extremely variable not only between individuals (Owen, 1970) but also for the same individual on different days (Morhardt and Morhardt, 1971). In some cases an increase in metabolism may not produce an increase in HR (Brush, 1965). However, Johnson and Gessaman (1973) found ample evidence to support

Figure 18. Relationship of metabolic rate and heart rate of winter brant in short-term tests.



the use of heart rate to predict metabolic levels of birds and mammals at rest or during moderate levels of activity. Owen (1969) has been successful in extending the use of HR for predictive purposes to a field situation for Blue-winged Teal (Anas discors) and Webster (1967) has done much the same with domestic sheep.

The HR is not useful for obtaining accurate metabolic information from animals under conditions of high metabolic demand (flight, cold, or heat) as has been shown by Berger, et al. (1970), Morhardt and Morhardt (1971), and others, since at these higher levels the metabolic rate and heart rate lose their linear relationship. These studies demonstrate what has been shown by earlier workers, that in activities or situations which are metabolically demanding, the oxygen requirements of tissue are more effectively served through change in oxygen pulse, and to a lesser extent stroke volume, than by an increase in HR.

As Owen (1969) has suggested, the present investigation of HR with T_A and MR is probably more valuable from a comparative than an ecological standpoint. Although not applicable to many "field situations", the heart rate information given here will be of value through providing an informational base for further investigations concerning determinations of energy relations of wild birds as indicated by HR.

Adult Energy Balance

The energy balance studies were conducted with Pacific Brant at summer T_A and photoperiod conditions similar to those encountered on the breeding grounds of the Yukon-Kuskokwim Delta.

Males used in the tests were heavier than females (Table 1),

however the mean weight of birds used (1319 g) was somewhat less than that of birds not tested (1488 g). The weight differences resulted from a progressive weight loss over the series, which occurred primarily between trials in the early part of the study. Cain (1973) has reported that caged Black-bellied Tree Ducks (Dendrocygnus autumnalis) used in his studies had lower mean weights than those of their free-living counterparts. In energy balance work with birds, an increase in body weight associated with a decrease in T_A is sometimes found, and among waterfowl has been reported for Canada Geese (Williams, 1965), Blue-winged Teal (Owen, 1970), and tree ducks (Cain, 1973).

Gross energy intake (GEI) and excretory energy (EE) have been reported to increase with declining T_A for the 3 waterfowl referred to above; the relation of GEI with T_A has been found to be linear in Canada Geese (Williams, 1965), Blue-winged Teal (Owen, 1970), and tree ducks (Cain, 1973), and the relation of EE with T_A is also linear except for the Blue-winged Teal where it is curvilinear due to a levelling off of values at lower temperatures. Regression lines describing the relationship of GEI with T_A may have different slopes and elevations for different photoperiods with the longest light period usually producing the most elevated curve, which results from a greater activity and longer maintenance of high body temperature (Kendeigh, 1969). The level of metabolism for Black-bellied Tree Ducks was higher on a 15 than on a 11 hour photoperiod (Cain, 1973). No opportunity was available to investigate the relationship of MR with varying photoperiod in this study.

Cain (1973) found no correlation between the caloric value of

feces and T_A in tree ducks, however, Owen (1970) found higher values at intermediate T_A and lower values at high and low T_A for Blue-winged Teal. Williams (1965) found a decreasing caloric value of feces with decreasing T_A. Over the range of T_A experienced by the Pacific Brant in this study, no change in caloric value of feces was observed.

Existence metabolism (EMR) is most commonly accepted to express the rate of utilization of energy by closely confined animals which are maintaining a relatively constant body weight over a number of days; EMR incorporates SMR, specific dynamic effect (SDE), and the cage locomotor energy requirement (Kendeigh, 1974). In contrast to SMR, the EMR vs T_A relationship is essentially linear throughout and no thermoneutral zone has been demonstrated, although for some species a flattening of the curve may occur at higher T_A (King and Farner, 1961). The range of T_A to which the caged-out-of-doors Pacific Brant were exposed was relatively abbreviated and did not extend below their established summer T_C of 4.3°C (see previous section). A minimum T_A of 10.8°C encountered during the trials precluded any possibility of comparisons below that value. Existence metabolic rates (i.e., also ME) found for caged birds from May through July (range, 161 to 364 kcal/bird·day) did not vary significantly and the mean value was found to be higher than those predicted for non-passerine birds by Kendeigh (1970) and by Dolnik (1974), by 83 and 25 percent respectively (Table 6). Values of EMR taken from the studies on Blue-winged Teal (Owen, 1970), Canada Geese (Williams, 1965), and Black-bellied Tree Ducks (Cain, 1973) are also considerably above those predicted. Kendeigh (1974) has

estimated that the increase of EMR over SMR should approximate 25 percent and this increase has presumably been included in his formula for predicting EMR on the basis of body weight.

Mean T_A reported by Mikkelson (1973) for the same period (May-July) on the Yukon-Kuskokwim Delta ranged somewhat lower (2.2 to 10.8°C) than those of this study. Existence metabolic rates for breeding ground birds would be higher than those found for captive brant, however not enough information is available to state what it might be.

The energy cost of free existence is a function of increased locomotor activity and must be added to EMR in order to obtain an estimate of total metabolism for free-living birds. This cost has been estimated by Uramoto (1961) to be from 30 to 50 percent greater than EMR for forest birds. Owen (1970) found that free, but not flying, teal had a requirement 13 percent above EMR, and on the basis of Owen's results Cain (1973) estimated the cost of free existence, including flight, of tree ducks to be a minimum of 25 percent. With an added 25 or 50 to cover the energy cost of free existence over and above EMR, the range of values for male and female Pacific Brant in summer would be from 306 to 367 kcals/bird•day.

Efficiency of utilization (EOU) values for male and female brant in this study were both approximately 60 percent, which is considerably lower than that given by Williams (1965) for Canada Geese (70-80), Owen (1970) for teal (75-80), and Cain (1973) for tree ducks (80-87). Type of diet or availability of dietary constituents is an important consideration influencing EOU, however the commercial feed formulae fed to the Canada

Geese and teal was similar to that given to the birds in this study and therefore the value of EOU for Pacific Brant seems inordinately low. On the other hand, a low commercial feed EOU for Pacific Brant may reflect an improper balance or nutrient composition contained in that diet compared with what the brant use naturally. It might be hypothesized that as the brant developed a use pattern for a marine nutrient resource, perhaps eelgrass exclusively, they evolved a nutritional dependence for it as well. Implicit in this thinking is that some modification in structure or function of digestive machinery, or absolute or relative nutrient requirements, etc., has occurred. Einarson (1965) expressed amazement at the voracity of brant feeding on Ulva sp., however this marine alga is not considered to be a preferred food source for brant and it may be that this behavior represents an increased intake due to poor efficiency of utilization.

The effect shown on GEI and EE by longer photoperiod is also demonstrated for existence metabolism. It has been shown, with exceptions, that existence metabolism at longer photoperiods is greater than at shorter photoperiods for the same T_A (Kendeigh, 1974). Longer photoperiods would naturally encourage extended activity and, consequently, increased energy expenditure and intake. Waterfowl, however, appear not to be as light restricted in their feeding as most birds which are normally considered to be diurnal in habit (pers. obs.). Williams (1965) reported some level of nocturnal activity for captive Canada Geese throughout the year in Illinois. In this study, with a 24 hour period of moderately fluctuating light intensity, brant had the opportunity to stay active

and feed continuously. Briefly, the longer photoperiod provides for increased time for activity and therefore maintenance of high T_B (longer periods of higher MR) which is balanced by increased intake. A continuous-light day with protracted period for activity, shown by the records, and food consumption explains the large discrepancy between observed and predicted rates for Pacific Brant, i.e. Kendeigh's (1970) formula for predicting EMR must be modified to compensate for local variation in day-length. A 4° change of latitude between Fairbanks and the Yukon-Kuskokwim Delta breeding area would not involve marked differences in photoperiod, although the light intensity pattern would vary between the two sites.

Gross activity recorded in this study accurately reflects that which occurs on the breeding grounds (C. Dau, pers. comm.) in summer, and personal observation bears out the records that the birds were not synchronous in their periods of rest and activity (Figs. 13, 14 and 15). A continuous pattern of activity under the constant light of subarctic summer such as was found in this study was reported for Willow Ptarmigan by West (1968). In contrast to this, activity of passerine birds under long light conditions are not uniform among the various species in that some exhibit a discontinuous pattern (Eyster, 1954; Karplus, 1952; Marshall, 1938; Aschoff et al., 1971) and others exhibit a continuous pattern (Palmgren, 1935; Eyster, 1954) for the same period and intensity of light.

Bird 2a in this study maintained weight over the first 2 trials, then declined food for the following three and in the last week the

bird demonstrated an intense and almost continuous activity pattern and was replaced. The intense activity exhibited by this individual, as a result of the stress it was apparently under, appears not to have markedly affected the randomness of activity of the two birds in the cages on either side.

Activity records for Canada Geese (Williams, 1965) and teal (Owen, 1970) maintained in central Illinois (42°N Lat.) show a bimodality during the mid-summer season, which became progressively less pronounced as the flight feather molt was initiated during the last of the summer and was then completely masked by nightly unrest during the premigratory period. Pacific Brant in this study did not undergo a flight feather molt until well after the trials were terminated and, as stated previously, only a low level contour feather replacement was in progress during the trials.

Summer Feed Study

Due to the difficulties involved in duplicating the diversity and frequency of food items used by feral animals, especially birds, few nutritional studies are carried out using natural diets. Where food items are known with any precision, there remains the necessity of procurring them in sufficient quantity for testing. The feeding habits and nutritional requirements of brant have been and still are generally controversial (Jones, unpubl.), however, when not on the breeding grounds in mid-summer, the diet of the Pacific race is reported to consist almost solely of eelgrass (Einarson, 1965) and little difficulty is encountered in collecting sufficient quantities for feeding purposes. This combination of factors, together with an

accessable supply of Pacific Brant goslings, allowed an opportunity for quantification of some aspects of the eelgrass-brant nutritional relationship. The feasibility of establishing a waterfowl marketing industry based on feeding eelgrass or eelgrass supplement was also of interest. The recent success of Bauersfeld et al. (1969) in increasing feed efficiency (FE) and rates of gain of domestic sheep on diets supplemented with turtlegrass (Thalassia testudinum) suggested that similar effects could be produced with waterfowl on eelgrass or eelgrass supplemented diets.

A survey of chemical constituents and caloric content of eelgrass from Izembek Lagoon, one sample of which represented material used in compounding diets, proved helpful in interpreting feed study results.

Due to the availability of fewer birds than required, plans to test 4 diets simultaneously using two groups of 5 birds each were modified to the extent that 3 diets were tested at one time. As goslings became incapacitated and/or died, the reduced numbers necessitated maintaining fewer birds in each group, consequently most groups tested, excluding those on commercial feed (controls), consisted of only 3 individuals; fewer problems developed within the control group and 10 birds were maintained throughout the study. It is not known what effect the different numbers had on the feeding behavior and efficiency of the groups, all of which huddled at the range of T_A's recorded (7.3 to 29.0°C). At T_A's below the T_C, huddling provides a significant saving for each bird but at higher T_A's no such benefit accrues (Kleiber and Winchester, 1933; Case, 1973). Case (1973)

also reported that energy costs were greater for Bobwhite (Colinus virginianus) in a covey than for individual birds when T_A's exceeded 5°C. The higher range of T_A's to which the birds in this study were exposed suggests that energy expenditures would have been greater for control birds than for birds on other diets and their efficiency therefore lowered. Efficiency differences resulting from unequal test group size were not measureable in this study. In addition, differences in rate and/or total consumption of food could have resulted from an allelomimetic effect (Penney and Bailey, 1970).

The effect of alternating diets in the test groups is unknown but presumably some impact would be made upon nutrient assimilation in the gosling brant. Weight recovery data for the goslings indicates that if a changed diet resulted in diminution of digestive capability it was of brief occurrence. Groups on the 50 percent test diet, although less than their normal weight level at 19 days regained normal body weight at day 28 and achieved an overall increase in body weight that was equal to the control group in the previous trial period (Fig. 16). In addition, Figure 16 shows that at a later date test groups having mean weights well below that of the control group, placed on commercial feed (ca. 33-35 days), had essentially regained the weight level of the control group when tests were recommenced on ca. day 42. Test groups, at the end of the study period, were generally emaciated and disheveled in appearance (Fig. 17), and were smaller in size and weight than control birds (Fig. 19). The poor appearance of test birds resulted in part from bathing in water pans containing eelgrass pellets which they carried

during feeding activities. After the trials had been terminated, and all the birds were fed commerical feed for 2 weeks, no apparent differences in plumage, size or body weights could be detected between the various groups.

Cannibalization occurred with greatest frequency in the pens where test diets were being fed. In retrospect, the problem is thought not to have been directly related to nutritional deficiencies of the 3 test diets per se, but rather to the decreased food intake and subsequent lowered resistance of the birds which created a situation favorable for injury. The goslings were especially vulnerable when blood quills were reaching full development and "wing drooping" was excessive due to their weakened state. Birds with ruptured blood quills were quickly set upon by the others and at least one bird displayed a propensity for habitual cannibalism.

A marked difference in caloric values of the various diets was found; commercial feed contained approximately 1 kcal per g more energy than 100 percent eelgrass. In terms of weight gain and efficiency, it is readily apparent that the birds were unsuccessful on 75 percent and 100 percent eelgrass (Table 4 and 16); this is probably a consequence of inadequate energy intake. Hill and Dansky (1954) found that chickens regulated their energy intake by increasing food intake when dietary energy was lowered. In contrast, this study indicates that, although the test diets had enough productive energy per kg of dry matter to meet minimum standards for starting, growing and breeding domestic geese (Merritt and Aitken, 1961), the brant goslings did not consume enough

Figure 19. Brant gosling from control diet group showing normal feather development and appearance.

of the test diets to meet their nutritive requirements. Immediately after the series was started the period of greatest remige growth for the gosling began. Energy requirements for rapid growth processes, such as flight feather development, became greatly elevated and the increased needs were apparently not met by dietary intake.

The 50 percent test diet appeared to be deficient during the early period of the series but appeared to have been of increasing value during later growth, suggesting that the energy intake was inadequate for growth and only marginally adequate for maintenance. Remige growth in adult moulters proceeds at the expense of other body tissues, especially muscle (Hanson, 1962). Findings of this study suggest that the former is true also for goslings and probably resulted in the early drop in body weight when dietary intake was inadequate on test diets.

Over the trial series no changes were observed in the caloric value of the excrement for each diet, indicating that no change occurred in basic ME values as well and the increased energy demands could only have been met by increasing food intake. Mean caloric values of excrement were only slightly less than the mean caloric values of 3 of the 4 diets. The mean caloric value of the feces of the 100 percent eelgrass test group was slightly greater than the caloric value of the diet (see Results). It is interesting to note that, although both groups consumed the same basic feed formulation having the same caloric value per gram of dry matter (4.811 kcals/g), birds in the adult energy balance trials were 5 times as efficient in removing energy (3.884 vs 4.605 kcals/g of excrement) as control birds

in this study. This difference in digestive efficiency may result from a decreased digestive function in goslings as compared to adults (Penney and Bailey, 1970; Holm and Scott, 1954) or the residence time of ingesta is shorter in the gut of goslings than in adults and otherwise available nutrients pass through the gut unabsorbed.

Feed efficiency and EOU values for birds fed 75 and 100 percent eelgrass diets are generally too low and few in number (Table 4) to merit lengthy comment. Brant goslings could not gain weight on the latter diets and only the 75 percent diet data showed a positive EOU, which was extremely low compared to the 50 percent diet, controls, and also adults in the energy balance study. The negative but increasing EOU values for the group on 100 percent eelgrass (Table 4) suggests an improved ability by goslings to use it as a source of nutrition, as one might expect for wild brant. In this study, as the percentage of eelgrass in the test diet decreased, the FE increased.

Feed efficiency of the control group decreased over the series and the 50 percent test diet group increased if day 3 data is disregarded; EOU's for these two diets were constant or decreased slightly. The EOU and FE trend shown for the control group indicates that, on a nutritionally adequate diet, the goslings become progressively less efficient as the energy demands for growth decrease and those for maintenance increase; a similar observation was made earlier by Brody (1945). A slight decrease in EOU is also shown for the 50 percent eelgrass diet group, however the efficiency for that group is only half that of the controls and reflects a lower metabolic performance. It is apparent that the 50 percent test

group was unable to fully utilize dietary energy and it is not clear why a decrease in efficiency over time, comparable to the control group should be found. Mean FE rates of control and 50 percent diets, although not significantly different statistically across the series, appears to be significantly different at the start of the series.

The generally poor results obtained from feeding test diets are attributed to low palatability; thus, the data in Table 4 show that food intake decreased as the percent of eelgrass in the diet increased. Reasons for low acceptability, or low palatability, are not known, however it is suggested that a high salt content (eelgrass was not washed prior to diet formulation) and unpleasant taste (personal appraisal) were possible reasons for rejection. As regards salt content, salt solutions approximating sea water salinity were largely unused by feeding adult birds even when fresh water was more remotely available, and birds lost body weight when salt water (ca. 3.5 percent by. wt.) was the only source of water.

Test diets were accepted better at the beginning of trials but consumption soon declined markedly. Fresh water consumption and carrying of test diet pellets to water by the goslings when feeding increased according to the percentage of eelgrass in the diet. Possibly NaCl loading may have been detrimental to the young birds, either through digestive dysfunction or through an inability to eliminate salt due to inadequate salt gland development. Wild brant foraging on natural beds of eelgrass probably do not ingest salt in great quantity because the straining action of the bill during prehension eliminates salt water

or in great concentrations because of dilution which likely occurs as a result of the release in the gut of cellular and extracellular fluids of ruptured plant tissue.

A less than adequate intake of protein probably explains why test diets failed to maintain the Pacific Brant goslings and the level of protein in the eelgrass used in the diets (sample 6-2-B, Table 5) was determined to be approximately 12 percent, lower than the minimum requirement for growing domestic ducklings (17 percent, Nat. Rsch. Council, 1971), for wild ducklings (19 percent, Holm and Scott, 1954) and for growing domestic goslings (20-22 percent, Orr, 1970).

The overall poor growth and development of the brant goslings when consuming test diets, as well as the results of the protein values obtained in the series (Table 5) are, in addition to being well below gosling requirements mentioned previously, below the 15 percent protein requirement of domestic breeders (adult geese) (Merritt and Ailken, 1961; Orr, 1970) and suggests that other foodstuffs of higher protein content are probably consumed by adult and young brant. Protein values given by Mikkelson (1973) for sedges and grasses reportedly used by goslings on the breeding ground are also below the minimum requirements given (see above); Mikkelson has also reported that young Cackling Geese, a congener of the Pacific Brant, used invertebrates heavily as food during early growth and development. A considerable epiflora and epifauna is found on eelgrass leaves at various times of the year, however the importance of that protein contribution to brant nutrition is not known.

A nutrient composition and caloric content series for eelgrass

collections made over a substantial period of time has not been reported previously, however proximate analysis of single collections have been reported by some workers. Protein values for eelgrass from Izembek Lagoon reported by Einarson (1965) are ca. 5 percent lower and those found by McRoy (unpubl.) are 1 to 6 percent higher than those found in this study. Burkholder and Doheney (1968) report a value of ca. 10.5 percent and Udell et al. (1970) give a value of 14.6 percent for the protein content of eelgrass leaves collected in waters adjacent to Long Island, New York. The highest protein value for eelgrass (19 percent) has been reported by Candussio (1960) for European samples. From these other studies it cannot be determined if the protein content of eelgrass fluctuates seasonally, the results of this investigation indicate that it does not fluctuate markedly. The range of caloric values given for eelgrass leaves from Izembek Lagoon by McRoy (1970) are similar to those given for the collection series in this study (Table 5).

Among the various nutrients in plants soluble carbohydrates, containing starches and other sugars, provides the major source of energy for birds (Fisher, 1972). The former is probably true for eelgrass also and throughout the collection series this fraction constituted a substantial percentage of the total nutrients which did not fluctuate markedly but was highest during the mid-summer period.

SUMMARY AND CONCLUSIONS

Growth and development of captive Pacific Brant in this study was extremely rapid in comparison with that of other waterfowl and is likely to have been accelerated above that of wild birds on the Yukon-Kuskokwim Delta and other breeding areas. The telescoping of the development period was thought to be responsible in part for an observed initial decrease in rate of weight gain which has also been recorded for other waterfowl. A second decrease in rate of gain which resulted in a plateau, occurred 5 to 10 days earlier than has been reported for wild brant, indicated a shorter development and potential earlier flight age than for wild goslings.

Perhaps the most interesting result of this aspect of the study concerned the growth rates of tarsi of brant which reached maximum lengths in a relatively abbreviated period. A rapidly developing tarsus in diving ducks has been considered as an adaptation for fast running water, however a strong positive correlation also exists between rate of development and increasing terrestrial habit. The brant, almost immediately after hatching, is associated with tidal waters and, as other geese, is a grazer as well. Thus it would appear that the brant may have benefited from two selective processes acting in concert, the result being that the tarsus reaches full development at an unusually early age.

The yearly weight curve recorded for brant in this study was thought to be fairly representative of that of wild populations to the extent

that it approximated general seasonal trends in weight change, although the levels of winter and summer were thought to be reversed with lowest weights recorded in April. At that time molt of flight feathers which normally occurs in August was also recorded. Geese normally reach lowest annual weight levels during the flight feather molt. A reversal of the summer-winter weight levels in captive birds is also indicated by a paucity of seasonal data on weights given by other workers for wild brant.

In order to determine the applicability of data gathered in this part of the study to the wild population, growth and development information should be gathered from wild young on the breeding grounds. In addition, in order to obtain an accurate picture of annual weight cycles of wild birds, weight data from transient brant must be gathered more systematically and more extensively than in the past. It is of course possible that more information for a yearly weight curve could be extracted from existing unanalyzed and unprocessed data held by waterfowl management agencies.

Unexpected seasonal differences in gaseous metabolism between summer and winter birds were found in this study. It is postulated that a circannual rhythm of molt was instrumental in brant developing lighter plumage in winter than in summer because the wild population is normally subjected to warmer winter than summer temperatures. Therefore, one would expect a higher MR at the same ambient temperature in winter due to an increased thermal conductance (decreased insulation) than in summer when insulation was increased. Another explanation which could be advanced is that the winter birds were still juveniles when first tested,

in contrast to a definite adult or subadult status when tested two years later. Conducting additional gaseous metabolism trials with adult birds in winter and further investigation into possible occurrence of circannual rhythms of insulation are suggested to help resolve this problem.

Heart rate information obtained for winter birds should have application in predicting metabolism in the field. Heart rate-metabolic rate investigations should be extended to include summer birds in order to determine seasonal differences and could be expanded through use of telemetered birds for the purpose of obtaining a more accurate definition of the relationship between SMR and EMR based on gaseous metabolism.

The adult energy balance study provided information on existence energy only in the thermoneutral zone. A wider range of temperatures should have been investigated. As stated earlier in the discussion, the temperatures to which the birds are exposed on the Yukon-Kuskokwim Delta during the mid-summer are somewhat below the T_C of the brant as determined in this study, consequently the information obtained does not reveal existence energy values at lower temperatures. A series of tests at different acclimation temperatures should be conducted in addition to those conducted outside under natural photoperiod and T_A.

If the ME and EOU values obtained in the adult energy balance trials were the same for eelgrass and commerical feed, this would allow an assessment of the impact of brant upon available food resources in their natural environment. Energy balance trials should be conducted with adult brant on diets of eelgrass in order to determine if an increase in digestive

efficiency over commercial feed would occur.

The poor results obtained in the gosling feed study are not readily explained, but do stimulate a great deal of speculation. It has been stated earlier that the major difficulty encountered in the gosling feed study was the unacceptability of the pelleted diet. Unacceptability was attributed to unpalatability, and it was suggested that this may have been due to an unpleasant taste or a high salt content; adult brant in captivity were noticed to avoid using salt water even when it was the only source of drinking water. Water used by the young brant on the breeding ground is brackish and thus they consume some level of salt from hatching, which would allow them to develop a salt metabolizing capability as well as a salt water use habit. It is suggested that the young brant in this study had neither the habit nor the capability of metabolizing the high salt concentrations of the diet. This latter may have been aggravated by the continued switching from test to control diets and back again. In order to find out if having a previous experience with a low-salt diet affects acceptability, all diets from the brant's earliest experience should be formulated with a relatively high salt content. In order to determine if unpalatability was the major factor in refusal of test pellets an additive could be used to improve the taste of all somewhat equally. In addition, an attempt should be made to investigate development of the salt gland in gosling brant to determine the rapidity with which it develops full excretory capability.

However, other difficulties in the brants' use of the eelgrass diets were also apparent from FE and EOU values. Again salt concentrations of

the diets may have been too great, for the reasons stated earlier. It has been found with some young birds that not having access to adult excreta prevents a normal microflora from developing in the gut, thus removal of the young brant from nests may have precluded the possibility of a microflora developing which would later allow efficient use of an eelgrass diet. If excreta is indeed the avenue of transfer of the necessary organisms, investigations should be conducted through use of excreta collected from the breeding ground and employed as an inoculum. A different, and more difficult approach would be to compare utilization of eelgrass between hand reared young and young captured from the breeding grounds at the age of about 1 month; the two groups would be assumed to have marked differences in their intestinal microflora. In this study, if the vestiges of a microflora for utilizing eelgrass existed in the gut of the young brant, switching of diets periodically may have prevented its full development.

Although cellulolytic activity has not been determined to occur in the digestive system of any geese, the brants' natural microflora may be the exception. It is recommended that microbiological and enzymatic assay be conducted for the intestinal tract and the cecae. Lengths of the cecae and small intestines should be compared between wild birds eating eelgrass and captive birds using commerical feed.

Another suggestion which has been made is that there might be a "factor" in sea water, or in the plant in the natural state, which is essential for an efficient use of eelgrass and unavailable to captive birds.

Low protein values found in the collection sample, which is representative of that used in compounding diets, may not be representative of the quality of natural material used by the brant as a selection may be taking place which casual collection by the investigator does not duplicate. Investigations of the material consumed by brant could be readily undertaken through collection and examination of folded leaves in digestive tracts.

It would appear also that during processing of the eelgrass material in this study, nutrient levels were lowered and some micronutrients may have been lost altogether. Available information indicates that other workers have found rapid loss of nutrients with certain methods of preparing sea grasses for analysis. Freeze drying would be the suggested preparation method for eelgrass for analytical purposes, and of course, for feeding as well.

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